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PLANKTON OF THE FLORIDA CURRENT. III. THE CONTROL OF THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE DAYTIME BY LIGHT AND TEMPERATURE

HILARY B. MOORE, HARDING OWRE, EVERETT C. JONES and T. DOW.[1]

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ABSTRACT

The four groups, pteropods, siphonophores, chaetognaths and copepods, have been studied separately and together in the plankton of the Florida Current. Vertical diffuseness of plankton was found to be under the control mainly of light at its upper levels and of temperatures at lower levels. This is true both within a population of a single species and, to some extent, between species living at different depths. Finally, in the copepods only, changes in level in response to temperature and light changes are superimposed on a seasonal change in level of the population which may be correlated with the presence of successive broods.

INTRODUCTION

In a study of the zooplankton of the Bermuda area (Moore, 1949), certain generalizations were made with regard to the behaviour and distribution of the organisms. The one to which the present work relates was the fact that the spread, or degree of vertical diffuseness, was slight in shallow-living species, but became progressively greater in deeper-living ones. In studies of the deep scattering layer and euphausids (Moore, 1950, 1952) it was shown that a workable explanation of the day-time vertical distribution could be obtained if it was assumed that two opposing factors were operative, temperature and illumination. During the descent and ascent periods of diurnal migration, illumination appeared to be the predominant control ex-

[1]Contribution No. 669 from Woods Hole Oceanographic Institution. Contribution No. 111 from the Marine Laboratory, University of Miami.

cept at the greatest depths reached. During the latter, that is to say around noon, temperature usually superceded illumination as the controlling factor.

Finally, in a study of the siphonophores of the Florida current (Moore, 1953), it was found that the mid-day level occupied by the various species varied in close correlation with the changes in level of the isotherms. In fact the regression of change in level of the species on change in level of the 15°C. isotherm was 95%.

The behaviour of very few marine plankton species has been studied, either experimentally or by deduction from field observations. Experiments have suffered from the great difficulties of reproducing natural conditions and obtaining consistent results. For this reason, or because of wide differences in specific behavior patterns, little generalization has been possible with regard to the characteristics of plankton as a whole. In the Bermuda studies, the characteristics of each species were determined, and the resulting data treated as a whole for correlation studies. It was felt that the generalized view so obtained clarified points not readily seen in studies of single species. In addition, of course, it greatly increased the amount of material available for statistical analysis. The same method has been followed in the present work.

Material and Methods

The field work, and part of the study of the material was carried out as a joint program of the Marine Laboratory of the University of Miami and the National Geographic Society. An account of methods used as well as of the hydrographic conditions observed, has been published by Miller *et al.* (1953). An account of the siphonophores has also been published (Moore, 1953). The study on chaetognaths is part of a doctorate thesis to be submitted by H. Owre at the University of Michigan. That on copepods, by E. C. Jones, was incorporated in part in a masterate thesis at the University of Miami, and that on pteropods, by T. Dow, is part of a masterate thesis to be submitted at the same university. The work on the individual groups is that of the authors indicated, while the coordination is that of the senior author. This coordinated study is part of an investigation of the scattering layer carried out by the Marine Laboratory for the Office of Naval Research under contract number NObsr-57146. It was also carried out in part at Woods Hole Oceanographic Institution under Bureau of Ships contract number NObsr-43270. The authors wish to express

their gratitude to all those members of both laboratories who have assisted in the work, and also to Mr. W. Shoemaker of Rochester Institute of Technology who helped greatly in obtaining the information on illumination.

A depth-distance recorder (Miller *et al.*, 1953) was used with all plankton hauls, and the counts of all species were corrected to a standard of one mile of towing. Generally, six or seven depths were sampled on each occasion. Owing to the strong currents in the area, it was not possible to hold the nets very close to a desired depth, but in general the water column was well sampled by a series of oblique hauls. The mid-depth of each haul was calculated, and from these, the depths half-way between each pair of hauls. It was assumed that each count was representative of the water column between two such half-way depths. The uppermost haul was assumed to extend to the surface, and the lowest, to the deepest recorded depth reached. For each species, and on each day, the total content of the water column was then integrated by cumulative multiplication of the counts and the lengths of the sections of water column to which they applied. A second integration was then performed from the top down, using the same figures, and the depths were noted at which 25, 50 and 75 percent of the above total were reached. In earlier work (Moore, 1949, 1953), the 50 percent depth so obtained was defined as the mean day level of the species, and the distance between the 25 and 75 percent levels as the spread. The mean day level, of course, varies widely in different species. In much of the present work it was convenient to eliminate the effects of such variation by expressing the values for each day as deviations from the annual mean for the species, the latter being the mean of all days for which data were available. In such cases, a positive value implies a depth greater than the mean, and a negative value, less than the mean. All depths are given in metres.

Only those species which occurred fairly consistently in adequate numbers, have been included. Not all these species were adequately represented on every day, so the numbers of pairs of figures available for comparison varies slightly throughout. The following species were included:

PTEROPODA

Limacina trochiformis (D'Orb.)
L. inflata (D'Orb.)
Creseis virgula Rang
C. acicula Rang
Diacria quadridentata (Lesueur)
Cavolinia longirostris (Lesueur)

SIPHONOPHORA

Chelophyes appendiculata (Esch.)
Diphyes bojani (Esch.)
D. dispar Chamisso & Eysenhardt
Eudoxoides mitra (Huxley)
E. spiralis (Bigelow)
Abylopsis eschscholtzii Huxley
A. tetragona Otto
Bassia bassensis (Quoy & Gaimard)

CHAETOGNATHA

Sagitta enflata Grassi
S. hexaptera D'Orb.
S. lyra Krohn
S. bipunctata Quoy & Gaimard
S. serratodentata Krohn
S. minima Grassi
S. decipiens Fowler
Pterosagitta draco (Krohn)
Krohnitta subtilis (Grassi)

COPEPODA

Neocalanus gracilis (Dana)
Undinula vulgaris (Dana)
Eucalanus attenuatus (Dana)
E. monachus Giesbr.
Rhincalanus cornutus (Dana)
Calocalanus pavo (Dana)
Euaetidius giesbrechti Cleve
Euchaeta marina (Prestand)
Scolethrix danae (Lubbock)
Temora stylifera (Dana)
T. turbinata (Dana)
Lucicutia flavicornis (Claus)
Haloptilus longicornis (Claus)
Candacia pachydactyla (Dana)
C. bispinosa (Claus)
Lubbockia squillimana (Claus)
Copilia mirabilis (Dana)
Acartia negligens (Dana)

At the station, approximately ten miles east of Miami, where this material was collected, the surface waters vary in origin. Water which has come through the Yucatan Channel is about 5°C. warmer than that from the Gulf of Mexico. None of the zooplankton species are restricted to one water mass only, although most show some relative variation in abundance in the two. The depth of the 15°C. isotherm was taken as a temperature standard. Its mean depth for the period was 151 meters, and its range, from 87 to 184 meters. The mean depth of the 50 percent level of the plankton, combining all species, was 93 meters. The selected isotherm is, therefore, deeper. However, the mean depth-temperature curve for the whole period was almost linear over the range of depths covered here, so the value of the standard temperature selected does not seriously affect the discussion.

Illumination was calculated by the method used in previous work (Moore, 1950), but making a small allowance for the effect of cloud.

The isolume selected was that with a value of 10^{-2}, which is approximately equivalent to one foot-candle. The mean depth of this for the period was 143 meters, and the range from 124 to 157 meters, which is considerably less than the temperature range. As with the 25, 50 and 75 percent levels of the plankton, the daily values for isotherm and isolume have, in most cases, been used as deviations from the mean for the period. Depths greater than the mean have a positive value, and lesser ones a negative value.

The Relation of Mean Day Level to Temperature and Illumination

Study of scattering layer records had indicated that, except in regions of slight temperature stratification, the mid-day level of the organisms concerned was likely to be under the almost complete control of temperature, with illumination exerting but little influence. An initial study of the Florida Current siphonophores showed a significant correlation between mean day level and the depth of the 15°C. isotherm. The regression of organism depth on isotherm depth was 95%. It should be noted that the latter figure differs from ones given later in the present paper since additional data have been incorporated in the present analysis. The coefficients of correlation between deviations from annual mean day levels and deviations of the depth of the 15°C. isotherm from its annual mean were worked out with the results shown in Table 1. The values are given for the four groups separately and for all species combined.

TABLE I

Coefficients of Correlation between Deviations of Mean Day Levels of the Species from their Annual Means and Deviations of the Depth of the 15°C. Isotherm from its Mean. Values with a Significance of P=>5% Are in Parentheses. P Is the Frequency with which the Observed Results Might Be Expected To Occur by Chance.

Pteropods	+.26
Siphonophores	+.33
Chaetognaths	+.24
Copepods	(+.04)
All species	+.18

Similar correlations between mean day level deviations and deviations in the depth of the 10^{-2} isolume showed no significant values, although the coefficient for the chaetognaths was sufficiently large to suggest the possibility of a relationship there. No significant change

was observed when the relationships to temperature and illumination were treated as partial correlations.

In the Bermuda work, no relationships were found between behaviour and temperature since there was so little day-to-day variation in the vertical temperature distribution. Night reaction to moonlight was rather closely correlated with the day level occupied by the species, but daytime reaction to cloudiness appeared to be a specific characteristic, not correlated with the depth of the species. It showed some correlation, however, with the extent of diurnal migration of the species, and the latter, in turn, was correlated with the depth of the day level of the species. In the Florida Current material, the closeness of correlation between day level deviations and isotherm deviations showed no relation to depth. On the other hand, it did appear to be a group characteristic. The pteropods did not give a significant value, probably because too few species were available for study. The coefficients were about the same, though, for pteropods, siphonophores, and chaetognaths. On the other hand, the copepods, with more data available than any other group, showed no correlation at all.

It is known that, in temperate waters, some chaetognaths and copepods change level seasonally (Russell, 1936). These level changes do not correspond with seasonal movements of either isotherms or isolumes, and appear to be specific characteristics of the successive broods, on which the adjustments of diurnal migration, and day-to-day level changes, are superimposed. It seemed possible that a correlation between day level and isotherm level might be masked in the Florida copepods by a similar seasonal rhythm. To test this possibility, partial correlations were calculated between deviations of day level and isotherm deviations, as well as between day level deviations and isolume deviations, but including a third variable, deviation from a given date. A series of six alternative dates was tested, namely the first of October, November, December, January, February and March. Of these, October 1 gave the highest partial correlation with change in day level, and was therefore used to recalculate the partial correlations of day level deviations with isotherm and isolume deviations. Allowing for the seasonal level change, these now became $+.57$ and $+.40$ respectively, both significant with a value of $P=<1$ percent. To demonstrate the nature of the seasonal vertical rhythm of the copepods, the partial regression coefficients of level deviation on isotherm and isolume deviations were calculated. These were $+105$ percent and $+81$ percent respectively. Using these factors, the effects of the daily

differences in isotherm and isolume depths were allowed for, and Figure 1 shows what the seasonal changes in day level of an average copepod would have been had there been no changes in temperature or light. The pteropod data were inadequate for such treatment, but

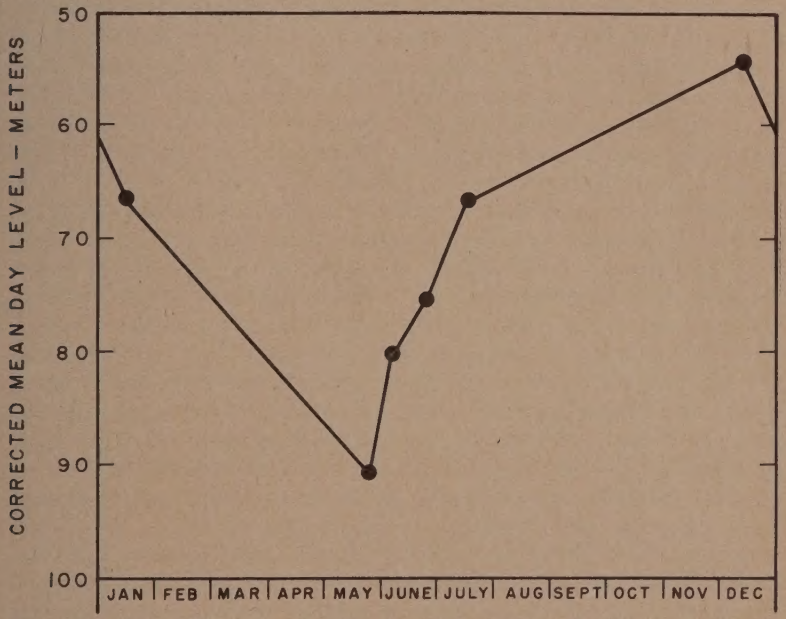

FIGURE 1. Seasonal variation in mean day level of copepods after correction for effects of variations in temperature and illumination.

neither siphonophores nor chaetognaths showed any significant seasonal level shift of this type. It remains possible, of course, that within these groups, individual species do show such a seasonal rhythm, but that these rhythms are not sufficiently similar in phase to appear as a group characteristic.

THE RELATION OF SPREAD TO TEMPERATURE AND ILLUMINATION

The vertical distribution pattern of a typical plankton species may be roughly represented by a kite, where the diameter of the figure at any depth corresponds to the concentration of the organisms there. In such a kite, the lower tail is characteristically longer than the upper part. A more accurate picture would probably be given if the sides

of the kite were skewed normal distribution curves. However, lacking adequate information as to the form of the curve, we have chosen the 25 and 75 percent levels as useful parameters for considering the outlying parts of the population. The distance between the two, or spread, has been used as an index of the diffuseness of the population.

The Bermuda data showed that, for all species combined, there was a significant increase in spread in the deeper-living species. This held true in the Florida material also, the correlation coefficient between spread and mean day level being +.44 ($P=<1\%$). The separate groups all showed positive correlations, but only that for the copepods was significant ($r=+.55$; $P=<1\%$).

In one group or another it has been shown that the degree to which the mean day level is correlated with temperature and illumination is itself dependent on the depth characteristically occupied by the species in question. It is probable, then, that a similar difference in reaction to these two factors exists at different levels in a population of a given species. Reactions at the 25 percent level may differ from those at the 75 percent level. If this is so, then variations in spread may be more simply explained in terms of reactions at the two limits which define it. Partial correlation coefficients were therefore calculated for each level with isotherm and isolume deviations. Significant values were obtained in most groups at one level or the other. Since we are concerned with the reaction of the plankton to movements of the isotherms and isolumes, it is clearer if the results are shown as regression coefficients. This is done in Table II, where the figures indicate the percentage response of the plankton to a given shift of an isotherm or isolume. For completeness, the responses of the 50 percent level also have been included. Since responses of the 50 percent level of copepods had been

TABLE II

COEFFICIENTS OF REGRESSION OF THE DEVIATIONS OF THE 25, 50 AND 75% LEVELS ON DEVIATIONS OF THE 15°C. ISOTHERM (ABOVE) AND OF THE 10^{-2} ISOLUME (BELOW). VALUES IN PARENTHESES ARE SIGNIFICANT WITH A VALUE OF $P>5\%$.

	Pteropods	Siphonophores	Chaetognaths	Copepods	All Species
25%	(+20%)	+32%	+ 36%	+ 62%	+ 22%
50%	+66%	+61%	+ 39%	+105%	+ 31%
75%	+71%	+76%	+ 41%	+151%	+ 42%
25%	— 7%	(+67%)	+116%	+ 75%	+137%
50%	(+10%)	(+21%)	(+ 84%)	+ 81%	+ 31%
75%	(+29%)	(+26%)	(— 52%)	(+ 22%)	+ 43%

found to be largely masked by the seasonal rhythm present, allowance has been made for this in calculating the partial regression coefficients in that group. Since, however, this seasonal effect has not been found in the other groups, the seasonal effect on copepods has not been allowed for in calculating the values for all species combined, and the values in this column are, therefore, probably somewhat lower than they should be. If the regression coefficients are considered as an index of the response of the plankton to changes in level of isotherms and isolumes, it is clear that there is a general tendency for the upper levels of the plankton to be more under the control of light and the the lower levels more under the control of temperature. This is not to be interpreted as a difference in response between shallow and deep species, since the effects of the differing characteristic levels occupied by the various species have been eliminated. The response differences exist between the upper and lower parts of the populations of a single species.

It appears that, if light penetrates deeper, the upper levels of the plankton move deeper also, but the lower levels show little response. On the other hand if the isotherms move upwards, the lower plankton levels move upwards, and there is little response in the upper plankton levels. The spread of the plankton is therefore related to the relative positions of isotherms and isolumes. To test this, the distance between the selected 15°C. isotherm and 10^{-2} isolume was calculated for each occasion. The deviations of this from its mean value for the period were then compared with the spread deviations with the results shown in Table III.

TABLE III

COEFFICIENTS OF CORRELATION (ABOVE) AND OF REGRESSION (BELOW) BETWEEN DEVIATIONS OF THE DISTANCE BETWEEN THE 15°C. ISOTHERM AND THE 10^{-2} ISOLUME AND DEVIATIONS OF SPREAD. THE PTEROPOD DATA WERE INADEQUATE FOR INCLUSION. ALL FIGURES ARE SIGNIFICANT WITH A VALUE OF $P=<1\%$.

	Siphonophores	Chaetognaths	Copepods	All Species
r	+.66	+.63	+.40	+.48
b	+ 95%	+ 89%	+ 51%	+ 62%

As would be expected, the copepods agree well with the other groups in this case, since their seasonal rhythm affects all levels together and not spread. With more data available, some seasonal rhythm might well be looked for in spread in all groups, since, in most areas, there is some seasonal change in the depths of both isotherms and isolumes. The present locality is unusual in that such

effects are likely to be masked by much greater changes due to water mass variation.

It was found, in Bermuda, that the spread of the plankton as a whole increased with depth. After elimination of the effects of isotherm and isolume movements, such relation was found also in the Florida material as shown in Table IV. Only the values for chaetognaths were not significant.

TABLE IV

PARTIAL CORRELATION COEFFICIENTS BETWEEN SPREAD AND THE 50% LEVEL OF THE SPECIES, OMITTING THE EFFECTS OF CHANGES IN ISOTHERM AND ISOLUME DEPTHS. THE VALUES FOR CHAETOGNATHS ARE NOT SIGNIFICANT, BUT THE REST ARE SIGNIFICANT WITH A VALUE OF $P=<1\%$. PTEROPOD DATA WERE INADEQUATE FOR INCLUSION.

	Siphonophores	Chaetognaths	Copepods	All Species
r	+.53	+.19	+.29	+.32

The regression coefficients were only small; —23 percent for all species combined.

A residual increase in spread with depth has been found. Spread is itself a resultant of differential movements of the upper and lower parts of the population. These upper and lower parts differ in the relative strength of their reactions to light and temperature. Some correlation may therefore be looked for between the strengths of these reactions of the upper and lower levels and the depths characteristically occupied by the species in question. For each species, the coefficient of regression of deviation of the 25 percent level on deviations of the 10^{-2} isolume were determined. The coefficient of correlation between these regression coefficients and the mean 25 percent level of the species was then calculated. It was significant only in the case of the siphonophores, with a value of $-.72$ ($P=<5\%$). Where the correlation was made with the 50 percent level of the species, the chaetognaths showed a significant value of $-.73$ ($P=2\%$). The direction of the correlation is as might be expected. The upper levels of a deep-living species tend to be less responsive to light changes than those of a shallow species.

A similar comparison was made between response to temperature at the 75 percent level and the 75 percent level of the species. Using regression coefficients, as above, no significant values were obtained. Using, instead, the coefficients of correlation between 75 percent level deviations and isotherm deviations, a value of $+.74$ ($P=2\%$) was obtained in the case of the chaetognaths. There is, therefore, some

indication that the lower levels of the population are more closely controlled by temperature in deep-living species than in shallower ones.

Discussion

The present study has been limited to conditions in the middle of the day when it is assumed that an equilibrium has been established after the morning descent. Scattering layer records indicate that such an equilibrium is rapidly established, and that, in fact, the organisms responsible for the phenomenon can migrate vertically faster than is needed to keep pace with the changing illumination. This is probably true also of even such small organisms as copepods, for which very rapid ascents and descents have been recorded. The basic data used were the levels occupied on different occasions by selected fractions of the plankton and by a selected isotherm and isolume. The three values being compared are, therefore, all depths. Within the range of depths under consideration, the rate of change with depth of both illumination and temperature is approximately linear. Changes in depth of isotherms and isolumes may therefore be considered as indices of the strength of temperature and illumination stimuli, and as having an approximately linear relation to them. It seems reasonable, then, to consider movement of the plankton in relation to movement of an isotherm or isolume as equivalent to a measure of response to a given temperature or light stimulus. Then a value of +100 percent, obtained as the regression coefficient of plankton movement on isotherm movement, indicates a response of the plankton exactly sufficient to maintain it under conditions of constant temperature.

In general, when some ecological condition of an organism is shown to be under the simultaneous control of two factors, and can be expressed as functions of each, then the condition resulting from the simultaneous variation of both factors is best expressed as the product of the two factors. In the present case it has been assumed that the deviation of the plankton level from its mean position may be considered as the sum of the movements which would have resulted had temperature or light operated alone. Whether or not this is strictly true is open to question, and will probably not be settled until more data are available. The assumption has, however, been made since it greatly simplifies the partial regression analysis. It can, however, be shown that the assumption that the reaction of the plankton is a function of the product of the temperature and illumination changes

results in values, the sum of the squares of whose errors is about four times that obtained assuming that the effects of the two factors are additive.

It is found that the mean day level of the various species studied followed the isotherm changes, but was influenced little, if at all, by light changes. This is in agreement with what is most usually found in the scattering layer in the North Atlantic. In the Mediterranean, where there is only very slight temperature stratification, this does not hold for the scattering layer. In Bermuda, where the temperature at the level concerned varied very little throughout the year, a correlation was found between the mean day level of the zooplankton as a whole and the cloudiness of the sky, but no more exact information on the vertical distribution of illumination is available.

Comparison of the responses of the plankton at its 25, 50 and 75 percent levels showed a transition from dominant light control at the top to dominate temperature control below. Three possible conditions are suggested which might produce such results. The responses of all the individuals in the population might be similar, and the observed vertical distribution might reflect either random "diffusion" around a center of distribution, or random movement more or less modified by the light and temperature conditions encountered away from this center. This is inherently unlikely since individual variation in reactions would be expected to occur in a population. The second alternative is that the observed vertical variation in relative reaction to light and temperature directly reflects the distribution within the population of individual reactions to these two factors. The distribution curves tentatively arrived at so far cast doubt of the likelihood of this. The third alternative combines the second with a modification of individual reaction by some third factor such as pressure. Further discussion of these alternatives must await considerable further analysis and probably calls for the examination of night levels also, and of the levels occupied during the morning descent and evening ascent.

When allowance was made for the effects of temperature and illumination on the 25 and 75 percent levels of the plankton, and through them on the spread, there still remained some residual tendency for the spread to be greater in deep-living than in shallower-living species. This agreed with observations in Bermuda. Furthermore, there was some slight indication that the upper (25 percent) levels are more responsive to light in shallow-living than in deep-living species, and conversely that the deeper-living species are the more responsive to

temperature at their lower levels. These two effects were, however, not universal.

Finally, in the case of the copepods, there was a residual seasonal change in level after variations due to temperature and illumination had been allowed for, and it was suggested that this resulted from different levels being characteristically occupied by successive broods, over and above any responses to temperature and light conditions. Such a seasonal vertical range has previously been demonstrated in a few plankton species.

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A REMARKABLE ASSOCIATION BETWEEN *OPHIONEREIS RETICULATA* (SAY) AND *HARMOTHOE LUNULATA* (DELLE CHIAJE).

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ABSTRACT

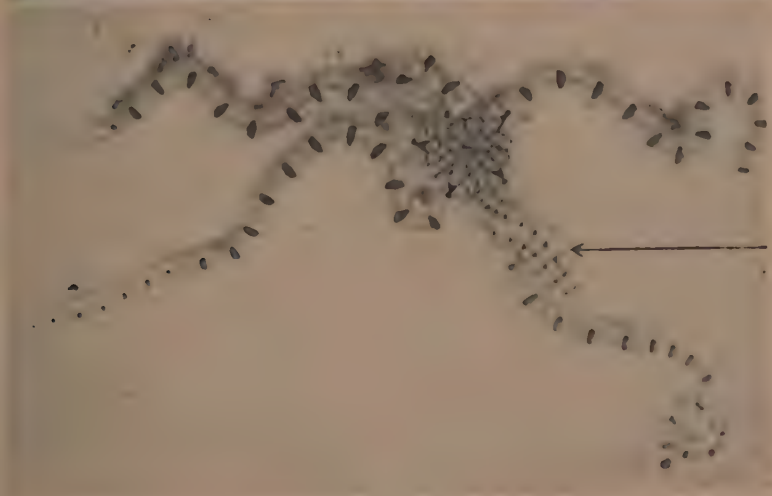
An association between the two forms is described. The associated animals were found on sand beneath a submerged stone on the shore near Kingston, Jamaica. The polychaete showed adaptation in its color pattern, which closely resembled that of the brittle star, and in its behavior, in clinging to its mate and seeking it out when they were separated. It would not associate with other species of ophiuroid. The ophiuroid showed adaptation in that its movements appeared to foster the association. Both forms were markedly negatively phototaxic.

Whilst collecting specimens from the breakwater at Port Royal, near Kingston, a specimen of *Ophionereis reticulata* (Say) was discovered in its usual habitat, beneath a submerged stone resting on clean sand, and with it was associated the polynoid *Harmothoë lunulata* (delle Chiaje). Since I have not observed this particular association before, nor yet been able to trace previous mention of it, and in view of several remarkable features, it was considered worthy of a report.

The photographs forming Figures 1 and 2 show the associated animals as they appeared in the laboratory. Two worms were associated with the ophiuran when captured. The larger, subsequently identified by Dr. Olga Hartman, remained immobile most of the time, wrapped around the aboral side of the disc of the brittle star, as shown in Figure 1. The smaller, apparently a very young form of the same species, remained concealed among the brachial spines.

Although the precise character of the association did not become clear during the two days that the animals remained alive, it must be noted that the mouth of the larger worm was located suspiciously near that of the ophiuran.

Occasionally, both polynoids made limited excursions along the arms of the ophiuran, and the larger is shown doing this in Figure 2.



FIGURES

The association between *Ophiomyces reticulata* and *Harmothoe luminata*.

FIGURE 1. (Above) Shows the polynoid wrapped around the aboral surface of the disc of its associate. X1.6.

FIGURE 2. (Below) Shows the polynoid (at tip of arrow) on one arm. X2.4.

On one occasion, it forsook its associate, rejoining it after some hours. If disturbed by mechanical stimuli, e.g., by turning the brittle star over, or by an increase in light intensity, the larger worm slipped quickly beneath the disc of its associate and remained totally concealed, only to emerge again later, or repeat the performance, when the ophiuran righted itself.

By night, the larger worm showed a bluish green luminescence in response to mechanical stimuli.

The form and color of the ophiuran appeared normal for the species, but, as will be evident later, it showed some signs of physiological adaptation to the association. The degree of adaptation, both morphological and physiological, of the polynoids was altogether greater.

In color, the worms matched the ophiuran very closely, being white, with a well defined repetitive black pattern borne on the elytra. The periodicity of the pattern differed in the two cases, however, there being three repetitions in the larger worm to two in the brittle star. Nevertheless, the degree of concealment achieved by the worm was remarkable, as will be clear from Figure 2. The tips of the parapodial setae were recurved to form a slight hook, which may be useful as a means of gripping the spines of the ophiuran, along the arms of which the worms were seen to move swiftly. Separation of the worms from the ophiuran could not be achieved even by vigorous shaking, and it was necessary to pick them off with fine forceps. After separation, the larger worm, normally quiescent, moved actively until it rejoined its mate, making a direct track towards it each time.

Although to merit stronger assertions much more observation and analysis would be necessary, physiological adaptations appeared to be shown by the following features of the association. First, it seemed specific, for when the larger polychaete was placed on, or near, other kinds of ophiurans, it avoided them, continuing to move around until it found its former associate. Second, both ophiuran and larger polynoid were remarkably phototaxic. An increase in light intensity brought about instantly a vigorous flight reaction in both, the former seeking to avoid the light by active locomotion, the latter by diving beneath the disc of its associate. Third, when contact between the associates was remade after separation, the ophiuran curved its arm so as to present as much surface as possible to the worm, enabling the latter to secure a better grip. Further, on similar occasions, it was observed that the brittle star sometimes folded its arms over the larger worm as if clasping it. If, by chance, the worm became wrapped

around a folded arm, this, unlike the others, was kept folded until the worm had moved along. As a result the worm was not flung off. However, it is noteworthy that the presumably sticky tube feet of the ophiuran were never observed to apply themselves to the worms, as might be expected if they were playing an active part in maintaining the association. There is a further point that should be considered. Since this species of ophiuran has been described as luminous, it is perhaps not without significance that the associated worm showed the same property.

Though this is, to my knowledge, the first instance of this particular association that has been described, *Harmothoë lunulata* is commensal with a wide variety of animal forms, a tendency that is well known among polynoids. The close matching in color and pattern of the worm and the ophiuran serves to emphasize further the variable color found in this species of *Harmothoë* and its tendency to simulate the color and pattern of its associates. The matching of color and pattern also recalls that described by Benham (1910) as existing between *Polynoë arenicolae* and *Polynoë pentactes* and their respective associates *Arenicola* and *Cucumaria.*

My thanks are due to Dr. Olga Hartman who identified the polynoid, and kindly supplied me with some information concerning its habits, and to Mr. Austin H. Clark, who kindly confirmed my identification of the ophiuran. I am indebted to Mr. Hansard Taylor, technician in this department, for Figure 2.

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ZOOGEOGRAPHY AND EVOLUTION IN THE OCTOCORALLIAN FAMILY GORGONIIDAE[1]

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ABSTRACT

The predominance of Gorgoniidae and Plexauridae in the shallow-water alcyonarian fauna of the West Indian and warm-water east Pacific regions is noted. The family Gorgoniidae is briefly characterized and its subdivisions down to genus defined. The subfamily designations Gorgoniinae and Lophogorginae are established. The nature of spiculation and external morphology is described and the significance of certain features in establishing an evolutionary sequence is explained. At the present time, two distinct lines of evolution can be detected within the family: one, well established and differentiated, characterized by simple spindle sclerites, centered as a whole in the American tropics but the most generalized species of world-wide warm-water distribution; and a second, less clearly differentiated but closely paralleling the development of the first, characterized by modified spicules, and limited to the Antillean region. The modern distribution is interpreted with the help of palaeogeography, which reveals Tertiary marine seaways through Central America. During the period of interoceanic communication, the homogeneous Atlantic-Pacific gorgonian population probably consisted of spindle-bearing species which had begun to undergo differentiation of branching pattern and were at the "anastomosed fan" level; spicular differentiation toward disk spindles had probably commenced also, since some Atlantic species have disk spindles nearly as well developed as those of typical Pacific Eugorgias. As the Pliocene wore on and interoceanic communication came to an end, the Gulf-Caribbean area apparently suffered changes in conditions that caused all but the hardiest species, or those in areas still reasonably favorable for gorgonian growth, to die out. In the subsequent ages, there has arisen from the small nucleus of undifferentiated species that survived, an entire new lineage which has flourished and now occupies as dominant a position in the shallow Caribbean waters as the relatively unchanged group from whose ancestors it arose still does in the eastern Pacific. It has followed much the same road of morphological development, but the physiological adjustment that the isolated eastern segment of the fauna achieved in the struggle for survival was accompanied by modification of spicule type from which developed the scaphoid sclerites that characterize all members of the lineage. That it is a newer group than the spindle lineage is suggested by the low level of differentiation between species. In the West Indian region the old spindle lineage now occupies a subordinate position and has not continued to develop as it has on the west coast of the Americas, where an extensive array of species has evolved.

Perhaps nowhere else in the world have the gorgonian corals at-

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tained such a prominent place in the coral reef fauna as they have in tropical American waters. Upon the Indo-Pacific reefs, which one thinks of as representing the very pinnacle of coral reef development, they are a minor element, largely replaced by their less elegant, though more ponderous, relatives, the Alcyonacea (Nutting, 1924, page 56). But on almost any reef or rocky bottom from Bermuda to Bahia, sea-fans and whips may be found in countless thousands, often comprising the most spectacular feature of submarine topography down to a depth of ten fathoms or so[2]. Likewise from La Paz to Peru they flourish, although true reefs appear not to be developed in this region (Galtsoff, 1950, page 27).

These vast gorgonian "sea-gardens" of the tropical Americas are made up almost exclusively of species belonging to but two families, the Gorgoniidae and the Plexauridae[3]. Certain peculiarities in the distribution of the gorgoniid genera prompted an investigation aimed at explaining these phenomena, and in the pages that follow I shall set forth the results and conclusions of this search. Before proceeding farther, however, it might be well to summarize the features considered in the classification of the Gorgoniidae, for the benefit of those not acquainted with the group, and to define my concept of the genera under consideration for those who are.

Since the earliest days of binominal systematics, when the Gorgoniidae included (as a genus: Linnaeus, Pallas, Ellis & Solander; as a family: Blainville; as an order: Lamouroux) practically all horny Octocorallia, the family has been restricted more and more until now it includes only those forms in which the calcareous spicules are less than 0.3 mm. in length, sculptured with regularly disposed girdles of complicated tubercles ("warts"), the anthocodiae are relatively unarmed, at most with but a few characteristically shaped flat rods *en chevron* beneath each tentacle, the horny axial cylinder is weakly loculated if at all, and is perforated by a relatively narrow, chambered central chord, and in which the branchlets are usually quite slender, with a thin cortex.

The basic spicule type, the symmetrical spindle with transverse belts of wart-like tubercles (Fig. 1, a), has been modified in various ways, and these modifications are the recognized criteria for the major sub-

[2] A. Agassiz, 1895, pp. 236, 237 (Bermuda); Nutting, 1895, p. 192 (Bahamas); Nutting, 1919, pp. 109-110 (Barbados); Hartt, 1870, p. 209 (Brazil).

[3] The genus *Muricea*, commonly considered the type of another family, actually belongs in the Plexauridae and has little to do with the other "Muriceidae" which are not reef-dwelling forms.

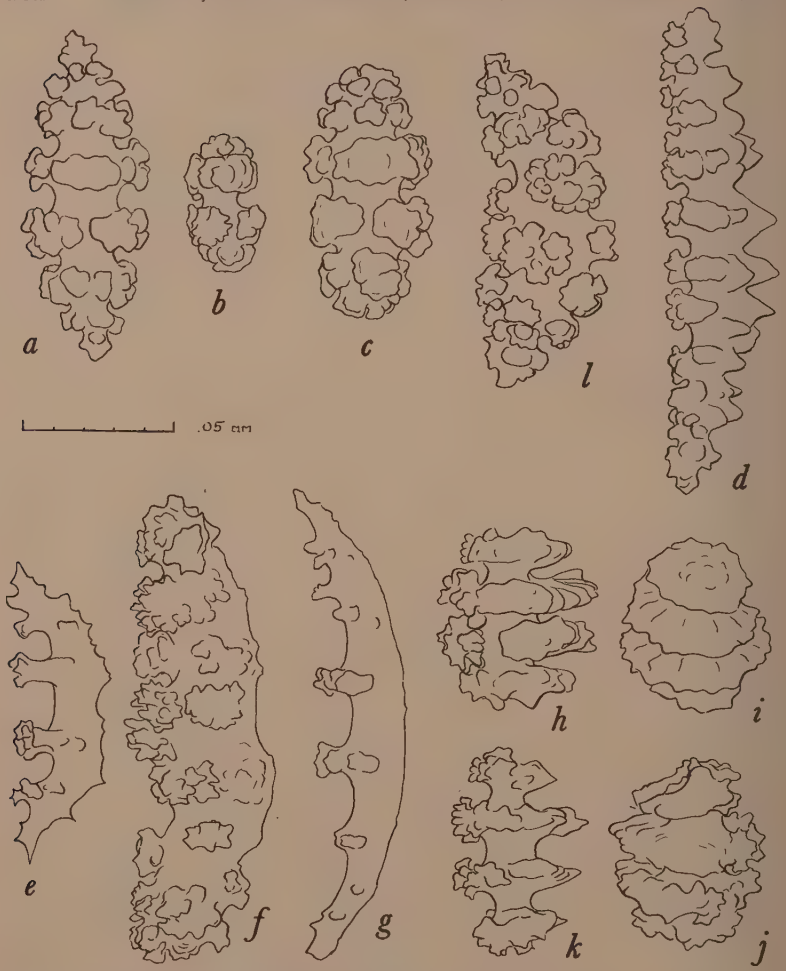


FIGURE 1. Gorgoniid spicule types.

a. Typical spindle of *Pacifigorgia media* (Verrill).
b, c. Short and long capstans of *Pacifigorgia media* (Verrill).
d. Unilaterally spined spindle of *Leptogorgia stheno* (Bayer).
e. Scaphoid of *Gorgonia flabellum* Linnaeus.
f. Scaphoid of *Pterogorgia guadalupensis* Duchassaing & Michelin.
g. Scaphoid of *Antillogorgia acerosa* (Pallas).
h-j. Disk-spindles of *Eugorgia rubens* Verrill. Profile and two oblique views.
k. Disk-spindle of *Leptogorgia viminalis* (Pallas) [=*L. virgulata* (Lamarck)]. Profile view.
l. Bent spindle of *Pacifigorgia media* (Verrill). Compare with true scaphoids, figs. e-g.

All figures drawn to the same scale, x420.

division of the family. The habit of branching, which shows progressive development from simple or sparsely branched whip-like forms, through bushy, pinnate and reticulate-flabellate facies, and finally to broad, leafy fronds, provides a series of characters useful in establishing generic limits. Variations in the size, sculpture and coloration of the spicules, in the form and arrangement of the branches, and in the secondary development of the coenenchyme, provide a basis for the classification of species.

Briefly outlined below is the subdivision of the family Gorgoniidae which is here recognized. A comparison with my earlier paper (1951) on the nomenclature of this group will reveal certain changes which have been made for zoological reasons brought to light by later studies.

Family Gorgoniidae

Subfamily Lophogorgiinae

The spicules are only straight spindles or derivatives, never canoe-shaped scaphoids (Klammern).

A. The spicules are all straight spindles with uniformly, symmetrically developed tubercles, and often also blunt spindles (capstans), likewise symmetrical.

1. *Lophogorgia* H. Milne Edwards & J. Haime, 1857. Type, *Gorgonia palma* Pallas, 1766 = *Gorgonia flammea* Ellis & Solander, 1786 [Cap de Bonne-Espérance], by monotypy.

   The branches are long and whip-like, or shorter and more or less distinctly pinnate, oriented in one plane, or bushy; in old colonies the branches may be somewhat flattened. [East Indies, northern Australia, west America, Caribbean, Mediterranean, east, south and west Africa; 30+ species.]

2. *Pacifigorgia* F. M. Bayer, 1951. Type, *Gorgonia stenobrochis* Valenciennes, 1846 [west coast of Central America], by original designation.

   The branchlets anastomose to form a fan-like network, in one plane. The spicules are capstans and simple spindles; the latter, if curved, never have the tubercles of the convex side reduced or absent (Fig. 1, l). [West coast of Mexico and Central America, including the Galápagos; Trinidad; Brazil; about 15 species.]

3. *Phycogorgia* H. Milne Edwards & J. Haime, 1850. Type, *Gorgonia fucata* Valenciennes, 1846 [west coast of Central and South America], by original designation.

   The branches are flat, foliate fronds with a lamellar axis. The spicules are blunt capstans. [Mazatlán to Chile.]

B. The characteristic spicules are spindles with the transverse girdles of tubercles fused to form disks, more or less eccentrically placed on the long axis of the spicule due to asymmetrical development (Fig. 1, h-j).

1. *Eugorgia* A. E. Verrill, 1868. Type, *Leptogorgia ampla* Verrill, 1864 [Margarita Bay, Lower California], by subsequent designation, Verrill, 1868, p. 386.

   The principal type of sclerite is the disk-spindle (the "double-wheels" of Verrill's descriptions); ordinary spindles with symmetrical sculpture are present in small numbers in some species. The anthocodiae are unarmed. [West coast of the Americas from southern California to Peru; 9 species.]

While this paper was in press, material of a *Eugorgia*-like gorgonian with anastomosing branches was received from Dr. Cadet Hand of the University of California. These specimens may justify the establishment of a new genus at the *Gorgonia-Pacifigorgia* level of development, and certainly suggest a continuing divergence of the disk-spindle offshoot in a direction similar to that taken by the spindle and scaphoid lines.

2. *Leptogorgia* H. Milne Edwards & J. Haime, 1857. Type, *Gorgonia viminalis* Milne Edwards & Haime, 1857 = *G. viminalis* Esper, 1791, ? = *G. viminalis* Pallas, 1766, = *Plexaura viminea* Valenciennes, 1855, = *G. virgulata* Lamarck, 1815 [in dem Hafen bey Charlstown in Süd-Carolina], by subsequent designation, Verrill, 1868, p. 387.

   The shorter spindles show more or less complete fusion of the tubercles of the transverse girdles into disks (Fig. 1, k). Near the branch tips, long spindles with tubercles unilaterally developed as smooth, conical processes (Fig. 1, d) are common; in the inner layer of cortex there are symmetrical spindles. The anthocodiae have a weak crown. [Southeastern states, Gulf of Mexico, Caribbean; 4 species.]

Subfamily GORGONIINAE

In addition to straight spindles there are modified forms, more or less canoe-shaped in profile, with the tubercles of the convex side undeveloped (scaphoids, Klammern or crampons; Fig. 1, e-g); disk-spindles are never present.

A. The coenenchyme may be somewhat flattened but it is not developed as broad expanded flanges with zooids in a groove along the edge, nor as querciform leaves.

1. *Antillogorgia* F. M. Bayer, 1951. Type, *Gorgonia acerosa* Pallas, 1766, by original designation [West Indies]. [= *Pterogorgia* of many authors, but not of Ehrenberg.]

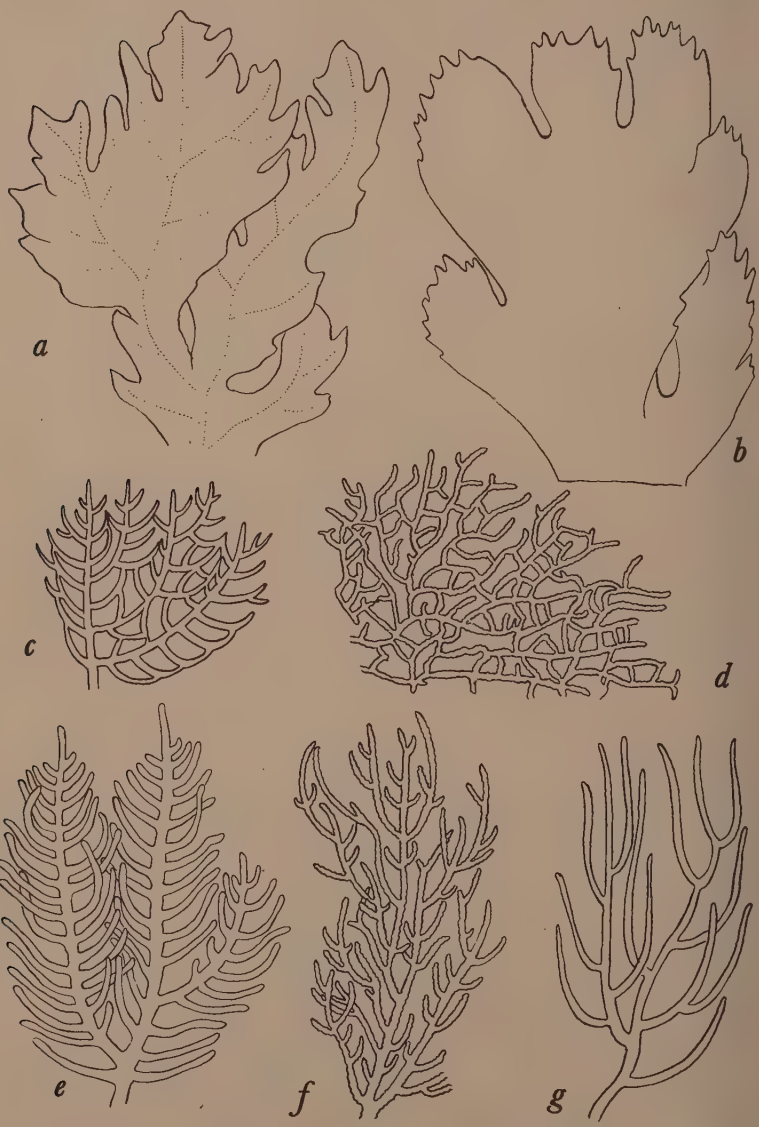
   The branchlets are pinnately disposed and more or less strictly in one plane. The major branches are in one plane or not, colonies often forming large, feathery bushes. The spicules are spindles and slender scaphoids. [Exclusively West Indian; 5 species.]

2. *Gorgonia* Linnaeus, 1758. Type, *Gorgonia flabellum* Linnaeus, 1758 [West Indies], by subsequent designation, Verrill, 1868, p. 386. [= *Rhipidigorgia* Valenciennes, 1855. Type, *G. flabellum* Linnaeus, 1758, by subsequent designation, Verrill, 1868, p. 385. In an earlier paper, I erroneously attributed this type designation to Bielschowsky, suggesting that the name could have been saved by a different choice. Obviously, however, the situation was already out of her hands, and the responsibility rests with Verrill.]

   The branchlets anastomose to form reticulate, fan-like colonies from which free twigs sometimes issue at right angles. The spicules are in the form of symmetrical spindles and stout scaphoids. [Exclusively West Indian; 1 certain, 2 doubtful species.]

B. *Phyllogorgia* H. Milne Edwards & J. Haime, 1850. Type, *Gorgonia dilatata* Esper, 1806 [das Meer des südlichen America], by original designation. [= *Hymenogorgia* Valenciennes.]

In this genus the horny axis is loosely reticulated but the coenenchyme is greatly expanded, filling in the meshes to form thin, flat fronds suggestive of oak leaves. The spicules are spindles and stout scaphoids. [Brazil; 1 species.]


a
b
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e
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g

C. *Pterogorgia* Ehrenberg, 1834. Type, *Gorgonia anceps* Pallas, 1766 [Mare Americanum], by subsequent designation, Milne Edwards & Haime, 1850, p. lxxx. [= *Xiphigorgia* Milne Edwards & Haime, 1857.]

The branching pattern in this genus is lax, openly whip-like or more bushy, depending upon habitat. The coenenchyme is expanded along the branches into two, three or four thin, longitudinal flanges into the edges of which the zooids retract. The spicules are very coarsely tuberculate, stubby spindles and scaphoids. [Exclusively West Indian; 3 species.]

These gorgoniid genera show a rather uniform progression in the complexity and specialization of the colonial form and of skeletal units, and it is most tempting to speculate therefrom as to their natural relationships, although the complete absence of palaeontological evidence reduces such speculations to the level of considered opinion.

The most significant feature of gorgonian colonies, from a systematic standpoint, is their spiculation, for the sclerites are less likely to reflect the effects of certain ecological factors upon the colony than are other structures.

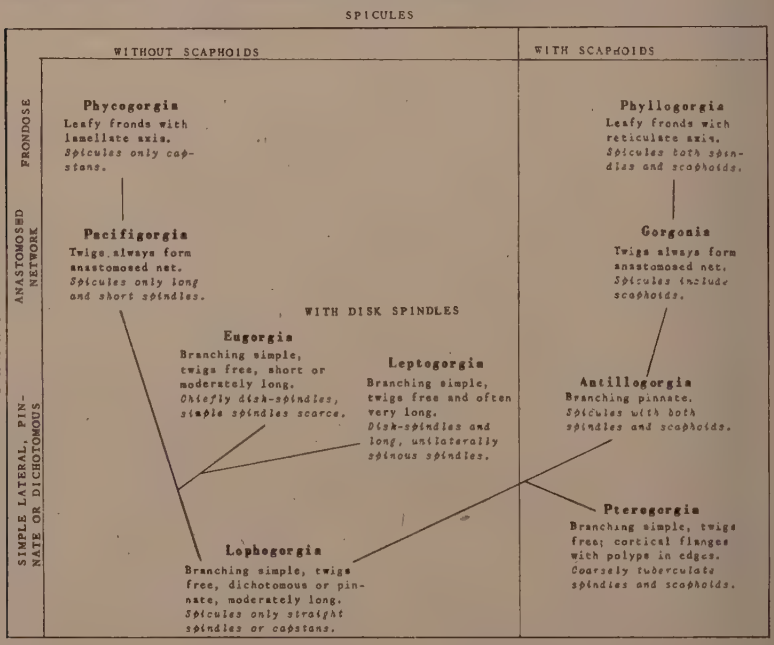
The simple monaxial rod more or less pointed at both ends (*i.e.*, a spindle) and ornamented with tubercles, spines or ridges, is a type of spicule found throughout the Octocorallia (except in the Coenothecalia, which lack spicules altogether). Although there are species which lack spindles in every order and probably in every family, they are few in number. The almost universal presence of this one spicule type is viewed as an indication of a primitive condition, and the de-

FIGURE 2. Branching patterns of gorgoniids.

a. *Frondose* with a weakly anastomosed, reticulate axis. One genus, *Phyllogorgia,* of the scaphoid lineage.
b. *Frondose* with lamellar axis. One genus, *Phycogorgia,* of the spindle lineage.
c. *Reticulate,* derived from the close-pinnate type. One genus, *Gorgonia,* of the scaphoid lineage.
d. *Reticulate,* derived from the open-pinnate type. One genus, *Pacifigorgia,* of the spindle lineage.
e. *Close-pinnate.* All species of *Antillogorgia* and some *Lophogorgia.*
f. *Open-pinnate.* Many species of *Lophogorgia,* some of *Eugorgia.*
g. *Simple lateral* or *whiplike.* Certain species of *Leptogorgia, Lophogorgia* and *Eugorgia* produce this type of colony. Its basic ramification may follow either a lateral (*i.e.*, very open pinnate) or dichotomous pattern; the end twigs may be greatly elongated. The branching of *Pterogorgia* (=*Xiphigorgia*) also follows this simple plan.

velopment of various modifications as representing evolutionary progression. These modifications, in the Gorgoniidae, are essentially four: (1) shortening of the axis with the number of tubercle whorls reduced to two, with terminal clusters (Fig. 1, b, c); (2) unilateral development of the tubercles of one side to form conical or spine-like processes (Fig. 1, d); (3) terminal bending of the axis, in one plane, to form a spicule canoe-shaped in profile with the tubercles of the convex side reduced or absent (Fig. 1, e-g); (4) the fusion of the tubercles to form disks (Fig. 1, h-k).

Superimposed on the spicular features is the gross morphology of the colony as a whole. This may reflect the effects of the external environment, especially of currents and wave action, although there are certain basic characteristics which apparently are never modified by the environment. Thus, a *Gorgonia* or a *Pacifigorgia* will always form a reticulate colony by anastomosis of the branches, though external factors may largely determine the size of the meshes, the diameter of the twigs, the growth of free lateral twigs at right angles to the plane of branching, or the production of secondary fans from the main flabellum. In general, the colonial form increases in complexity from a simple whip, through openly branched (Fig. 2, e-g) to reticulate forms (Fig. 2, c, d), ultimately reaching the frondose development characteristic of *Phyllogorgia* and *Phycogorgia* (Fig. 2, a, b).



In the representation given above, the genera are arranged in order of complexity of growth form, from the simple, open pattern of *Lophogorgia* to the leafy fronds of *Phycogorgia* and *Phyllogorgia*. The right half of the diagram shows the scaphoid-bearing genera of the Atlantic, the left half the spindle genera of predominantly Pacific distribution. Perhaps the divisions appear to be founded on relatively minor variations, still it is even more obvious that the only alternative, to treat all of these genera as mere variations within an all-inclusive *Gorgonia,* would be a century's stride backward from reality.

Virtually nothing is known about the environmental factors which govern the distribution of Gorgonacea, although something can be inferred from a comparison with the stony corals. A suitable solid support is required (only a few deep-sea species can adapt themselves to life upon both rocky and muddy bottoms) and if it is not present, planulae presumably will not develop (Cary, 1914, page 84). The chemical composition of the seawater is unquestionably important in restricting gorgonian distribution, and the variations in salinity, oxygen content, and other critical factors, which gorgoniids can tolerate are probably about the same as for hermatypic scleractinians, the distribution of which roughly corresponds to that of the Gorgoniidae in general. Heavy sedimentation is not conducive to a flourishing gorgonian population, at least in the West Indian region. However, just as some Scleractinia can live in muddy water, there are species of gorgonians which thrive in conditions probably intolerable to most reef species. Notable among these is the common *Leptogorgia* of inshore waters from Chesapeake Bay south to Texas, which flourishes in perpetually muddy water. Perhaps the one most important feature in distributional control is temperature, and it may well be instrumental in maintaining the peculiar disjunct distribution characteristic of such species as *Leptogorgia virgulata* and *Muricea pendula*. These species, along with numerous other invertebrates, are now absent from the southeastern part of peninsular Florida though specimens from the upper Gulf coast are indistinguishable from those from South Carolina. These were probably continuous populations when Florida was under water, even though some factor, probably temperature, now keeps the two moieties from rejoining along the present day lower Florida coast. Whether the free-swimming planula-stages of *L. virgulata* and *M. pendula* are of sufficiently long duration for offspring of the Gulf populations to become established on the Carolina coast, and

thus contribute genetically to the populations of that region, is unknown.

The Recent distribution of gorgoniids is rather narrowly limited. With the exception of *Lophogorgia,* which occurs also on both coasts of Africa, in the Mediterranean, and in the East Indies as well as in the Americas, it is exclusively a tropical American family. The scaphoid-bearing group of species is restricted to the West Indian region, while the group lacking scaphoids is principally west American. As nearly as I have been able to determine, there are about 27 species of *Lophogorgia,* 22 of which occur on the Pacific coast. Since the African and East Indian species do not occur in American waters, they will not be considered further. This genus alone of all gorgoniids now enjoys a wide distribution, but even it is nowhere rich in species except on the west coast of Central America. The known gorgoniid genera displaying any degree of specialization are exclusively tropical American, both Atlantic and Pacific. One possible conclusion to be drawn from this observation is that a relatively primitive *Lophogorgia* was once widespread, but has continued to flourish and differentiate only in those regions particularly suited to its development, the Americas. Of course, it is also possible that all of the genera were formerly of wider occurrence, but have lately died out except in American waters. Were this the case, however, we should expect to find traces of the other genera along with *Lophogorgia* in widely separated localities. Perhaps we shall, but since the days of great explorations have come to a close without their being found, their discovery now seems improbable.

There appear to be upwards of 60 recognizable species of Gorgoniidae at present living on the two coasts of the Americas and in the adjacent islands. Most striking is the fact that all of the species characterized by the peculiar canoe-shaped spicules called scaphoids are confined to the Caribbean area. Similarly, those species with strongly modified disk-spindles and few symmetrical spindles are found only on the Pacific coast, while those with the disk-spindles moderately developed and abundant unilaterally spinous spindles are entirely Atlantic. The genus *Pacifigorgia,* especially well developed in the Gulf of California and Panama Bay, has been found only in the eastern Pacific, with a single exception—which occurs in Trinidad.

A preliminary tally shows that on the Pacific coast there are 22 species of *Lophogorgia,* 14 of *Pacifigorgia,* 9 of *Eugorgia,* and 1 of *Phycogorgia,* whereas in the Atlantic *Lophogorgia* is represented by only 5 species and *Pacifigorgia,* by a single relict species. The strictly

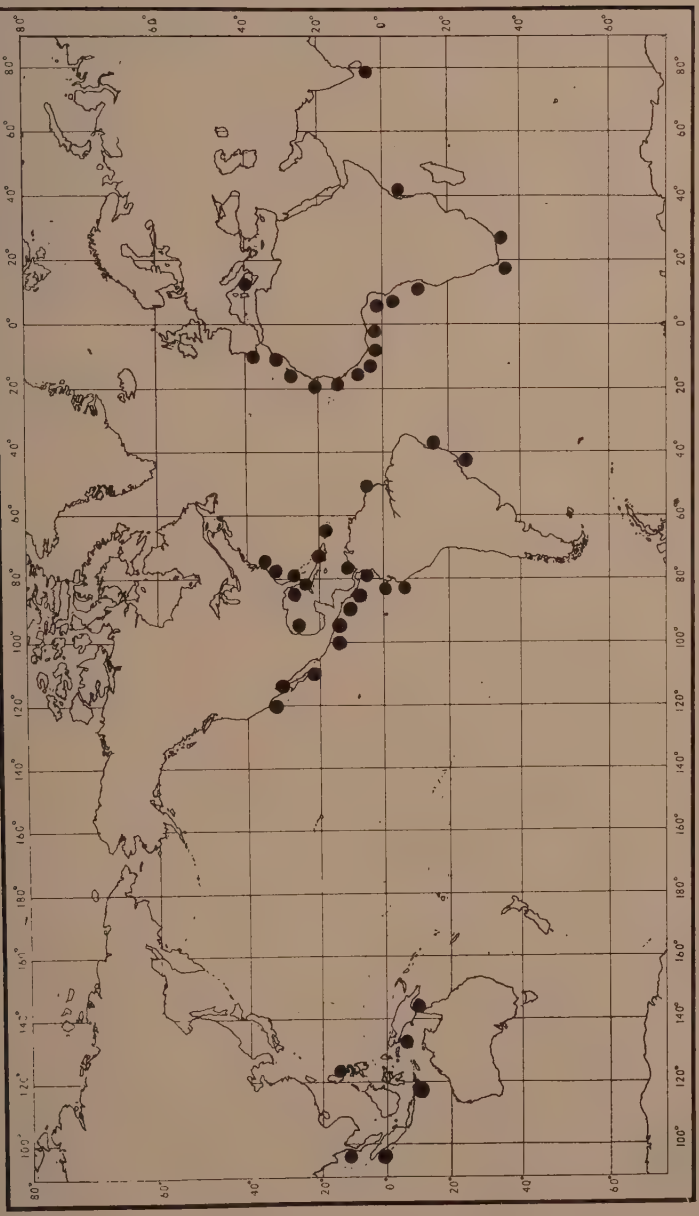


FIGURE 3. Geographical distribution of the gorgoniid genus *Lophogorgia*.

Atlantic genera *Antillogorgia, Gorgonia, Phyllogorgia, Pterogorgia* and *Leptogorgia* are represented by 4, 1, 1, 3 and 4 species, respectively.

Even though there is no published palaeontological evidence to assist in the interpretation of these observations, the palaeogeography of the Caribbean region is significant. Schuchert (1929) points out that there was open communication between Atlantic and Pacific (and thus the faunas were potentially continuous) in two places at different times. The earlier of these was the Panama-Costa Rica marine portal, which opened late in the Eocene and finally closed at the end of the Miocene, a period perhaps in excess of 30 million years (Knopf, 1949). Evidence is conflicting, however, and it is thought possible that the Panama-Costa Rica area was emergent during most of the Oligocene, so that the oceanic portal may only have been open during the late Eocene and again in Miocene time. Perhaps more significant to the present study is the later, more northerly Tehuantepec portal. Of it Schuchert says, "However, another but short-lived marine portal came into existence, this time to the north of Central America across the Isthmus of Tehuantepec. It was certainly open during early Pliocene time and probably also during the late Miocene, permitting the marine faunas of the Gulf of Mexico to spread west and thence north into southern California." (Page 341.)

A recent communication by Durham, Arellano and Peck (1952), read before the annual meetings of the Geological Society of America, denies the existence of any Tehuantepec seaway in the Cenozoic. Dr. Wendell P. Woodring tells me that he has never accepted the idea of a portal at the Isthmus of Tehuantepec, but that interoceanic communication across the Panama-Costa Rica region during the Tertiary is a certainty. For the purposes of marine faunal interchange, and probably also of ecological alteration in the Caribbean and the Gulf of Mexico, the portal in lower Central America is entirely adequate.

Let us consider what is known of the modern distribution of gorgoniid genera in the light of the palaeogeographical picture. Since the species at the lowest level of development, which we refer to by the generic name *Lophogorgia,* are still generically undifferentiated on the two sides of Central America, it is inescapable that they represent a once continuous population for there is no possible way they could have spread from the one ocean to the other after the final, complete emergence of Central America. The same holds true for the genus *Pacifigorgia,* which represents a more advanced grade of specializa-

tion, but in this case there is only one relict species in the Atlantic though fourteen still persist in the Pacific. From this it is possible to conclude that a newly evolved, more specialized, less tolerant group was all but wiped out in the Atlantic by changed conditions resulting from closure of the portals. If the more highly developed, foliate *Phycogorgia* had come into existence while there was still free interoceanic communication, the Caribbean population did not survive the conditions accompanying isolation from the Pacific segment.

The spatial and temporal distribution of some scleractinian genera serves to substantiate the observations outlined above. The genus *Acropora,* which has numerous Pacific species, is represented in the Caribbean by only three; and *Pocillopora,* likewise a prominent reef form of the Indo-Pacific area, including the warm-water East Pacific, is now entirely absent from the Antillean region. Both genera are better represented in the Tertiary deposits of the Antilles and southeastern United States, showing that one genus has suffered regression to some extent in this area, while the other has died out entirely. About the Acroporas Prof. John W. Wells (personal communication) has the following to say: "It would appear that there was a wider diversity of species in the Tertiary in the West Indies, and that some species-groups, still flourishing in the Pacific, have died out." Other genera showing similar distributional patterns could be mentioned.

Leptogorgia and *Eugorgia* are closely related genera both of which have modified spicules in which the transverse whorls of tubercles are solid disks instead (Fig. 1, h-k); however, since *Leptogorgia* has highly characteristic, unilaterally spined spindles (Fig. 1, d) which *Eugorgia* lacks, it seems likely that it represents a new offshoot of the *Eugorgia* stock, each genus now having diverged from the ancestral type. The scaphoid-bearing genera, *i.e.,* the entire subfamily Gorgoniinae, are absolutely restricted to the waters of the western Atlantic. Extensive collections from the Gulf of California and the Bay of Panama have failed to yield a single specimen which has scaphoid spicules. Neither has any scaphoid species been recorded in the literature from the Pacific coast, and the few references from the Australian region appear to be based upon a misinterpretation of spindles as scaphoids. The late Professor G. Stiasny (1951, pages 32, 49, 50) recently recorded *Pterogorgia peruana* Stiasny and *Pterogorgia* sp. (now *Antillogorgia*) from the coast of Peru, but it should be observed that these records, like those of *Phycogorgia fucata* (Valenciennes) and *Gorgonia stenobrochis* Valenciennes (now *Pacifigorgia steno-*

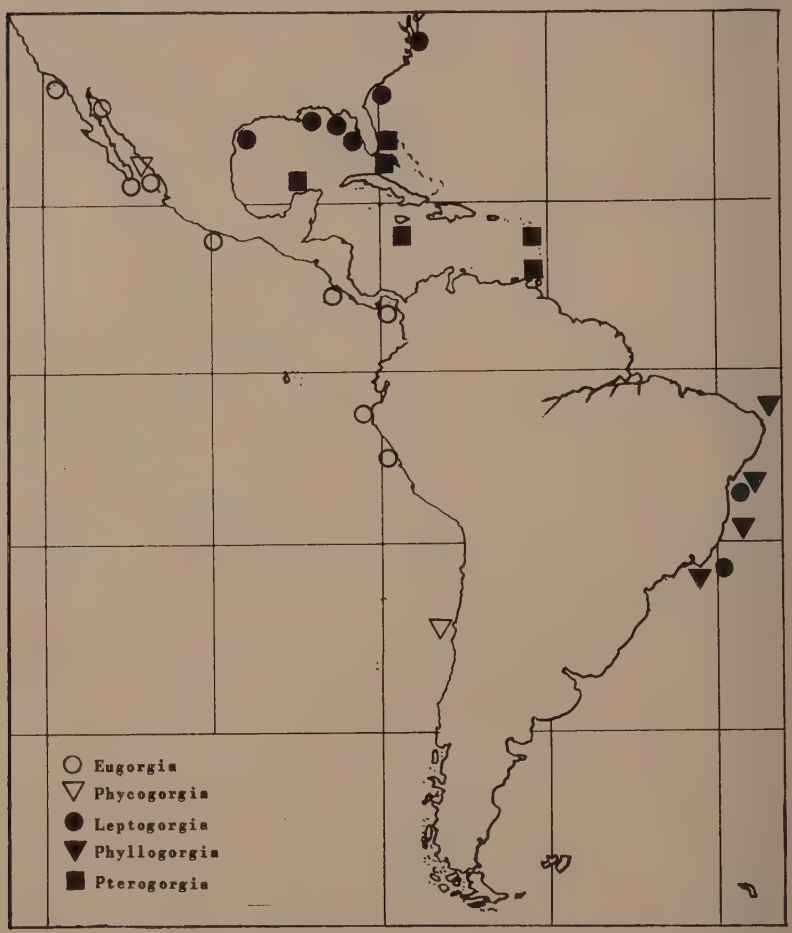


FIGURE 4. Geographical distribution of the gorgoniid genera *Eugorgia, Phycogorgia, Leptogorgia, Phyllogorgia,* and *Pterogorgia.*

brochis) from New Zealand, which he also perpetuates, are based upon very old material gathered in times when the mixing of labels was a commonplace. It is most improbable that these specimens grew where their labels indicated, and their appearance in the literature at this late date is not considered a serious threat to any suggestions advanced

FIGURE 5. Geographical distribution of the gorgoniid genera *Pacifigorgia, Gorgonia* and *Antillogorgia.*

in the present paper.

It is a most inviting conclusion that the scaphoid genera evolved from remnants of the older spindle group after the final closure of the Tehuantepec Portal. It seems almost beyond question that circulation of water in the Gulf of Mexico and Caribbean Sea was changed,

perhaps radically, by the closure of the portals, and other features of the physical environment probably changed with it. Such changes may well have been sufficiently far-reaching to cause the regression of even the stable genera and to stimulate the production of new evolutionary trends through the selection of mutations better adapted for survival in the new surroundings. It is interesting to note that the grades of development within the (presumably younger) scaphoid lineage are almost exactly parallel with those of the older, simple spindle lineage, and that the species are not only fewer in number but less clearly defined. At the simplest level of colonial form (*Antillogorgia*) there are but four, perhaps five, good species (though a number of others have been described). Of the more advanced, reticulate form, only one species is at present recognized, though there appear to be incipient species which critical study may enable us to distinguish accurately. It is impossible to assign systematic significance to the various growth forms of *Phyllogorgia,* and only a single species can be recognized. *Pterogorgia* (the *Xiphigorgia* of most authors) appears to be an early divergent offshoot of the scaphoid line. It contains three closely related species that are restricted to the Antillean region.

An interesting parallel can be drawn between this apparent evolutionary series in the Gorgoniidae and that of some fossil scleractinians as described by Lang (1938). This author held that a number of well-established genera of corals which cut across geological time also spanned more than one evolutionary line. In short, these genera represented the members of different lineages at similar levels of evolutionary development. Thus, a given species in genus "A" could be more closely related to a contemporary species in another genus, "B," than to a third placed in genus "A" but which actually belongs to a different lineage in a higher stratum. Lang proposed to retain these polyphyletic "genera" as a matter of convenience, under the name "genomorph," written in braces between the true generic and specific names. Since the gorgoniid scaphoid lineage is apparently derived from, and younger than, the spindle lineage, and is now isolated from it by a geographical barrier which may be taken to represent time, the evolutionary trends within this modern group seem to approximate closely the situation described in the fossil corals. There was a time in the history of gorgoniid nomenclature when externally similar but unrelated species were placed in the same genus, a situation which thus takes on the character of genomorphs. For example, Valenciennes (1855) established the genus *Rhipidigorgia* for a number of net-like

species (not all gorgoniids), and for a time this name was used by Verrill for both the Atlantic and Pacific reticulate Gorgoniidae which have been shown to be generically distinct and evolving separately. If we used the genomorph system of retaining the old genera, we should have to write *Gorgonia* |*Rhipidigorgia*| *flabellum* Linnaeus and *Pacifigorgia* |*Rhipidigorgia*| *adamsii* (Verrill). It would obviously be pointless, indeed unthinkable, to use any sort of genomorphic nomenclature to preserve antiquated generic concepts which modern methods of investigation have shown to be groundless. Such a system may be useful to palaeontologists, but its application in systematic zoology is questionable.

In review, we have seen that the family Gorgoniidae comprises two virtually parallel lines of development, each clearly showing three major evolutionary grades and some minor divergences. One of these lines, which we have called the "scaphoid lineage," is restricted to the tropical western Atlantic, has relatively few and poorly differentiated species, and is thought to represent a newly developing group. The other line, the so-called "spindle lineage," is found in warm seas around the world, has numerous (especially on the Pacific coast of the Americas) species which are more clearly defined, and is thought to represent an older stock from which the scaphoid lineage has developed. The presence of the most generalized genus of Lophogorgiinae on both shores of the Americas can be explained most satisfactorily in terms of an Atlantic-Pacific oceanic portal, which geologists consider certain. The recession of all advanced Lophogorgine types in the Caribbean to a single relict species, and the establishment of an entirely new line of evolution are attributable to the influence of ecological changes brought on by closure of the portal.

Acknowledgements

In the present day, when so much of real value is being written about such theoretical aspects of biology as evolution, one hesitates to add to the mass of worthy literature any observations not solidly based on confirmable fact. So much of zoogeography depends upon the vagaries of collectors, and so much of palaeogeography depends upon the interpretation of fossil evidence, that it may seem foolhardy to reconstruct with their help the possible evolution of a group which itself lacks a good fossil record. Should these suggestions prove invalid, as well they may, still their refutation may cause someone to learn something new and all will not have been lost. For the encour-

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UNDERWATER SOUND PRODUCTION AND CONCURRENT BEHAVIOR OF CAPTIVE PORPOISES, *TURSIOPS TRUNCATUS* AND *STENELLA PLAGIODON*.

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ABSTRACT

Characteristic sounds in the sonic range made by captive dolphins, or porpoises, were heard and recorded using underwater listening gear. The phonations described include those elicited by strange objects, those which accompany feeding activity, a distinctive sound heard during the mating season, and others less clearly associated with particular circumstances or stimuli. *T. truncatus* is highly vocal, a characteristic which may apparently be related to certain behavioral traits and to its usual coastal or inshore environment. On the other hand, only two types of phonation have definitely been attributed to *S. plagiodon*, an offshore species whose behavior differs in many respects from that of *Tursiops*. Previous accounts of porpoise sounds and the circumstances attending their production are reviewed.

It has long been known that some, at least, of the toothed whales are capable of emitting characteristic sounds under water, but the significance of this subsurface phonation is still largely a matter for conjecture. Schevill and Lawrence (1949), using underwater listening gear, heard and later recorded (1950) a remarkably wide variety of sounds from the beluga or white whale, *Delphinapterus leucas*, which is nicknamed "sea canary." Kullenberg (1947) and Fraser (1947) describe whistling sounds made by the common dolphin, *Delphinus delphis*, swimming alongside ship; Fraser remarks that these whistles ranged above the upper limit of his hearing, though it is not stated how this was ascertained.

The small cetaceans maintained at Marine Studios, Marineland, Florida, have been the subject of a number of published accounts. McBride (1940), McBride and Hebb (1948), and McBride and Kritzler (1951), writing about the permanent colony of bottlenosed dolphins or porpoises, *Tursiops truncatus*, mentioned three distinctive sounds that could be heard through the sides of the porpoise tank without the aid of any underwater listening device. To some extent it was possible for these authors to correlate two of the sounds with specific situations or with some particular behavior on the part of the

porpoises. These accounts will be considered in more detail below.

In the course of his observations on the young pilot whale, *Globicephala macrorhyncha,* at Marine Studios, Kritzler (1952), using a hydrophone, distinguished at least three sorts of sounds produced underwater. Kritzler noted that two of these sounds, whistling and a "peculiar grating snore," were similar to sounds made by the porpoises.

Recent investigations into the frequency range of sound production and auditory sensitivity in porpoises put a new aspect on the question of the significance of odontocete phonation. Kellogg and Kohler (1952) found evidence that *Tursiops* can detect ultrasonic vibrations up to at least 80,000 cps, approximately 60,000 cps beyond the range of human hearing. Schevill and Lawrence (1952), working with an adult female *Tursiops* at Marineland, collected data indicating that this animal could detect signals above 100,000 cps. Moreover, the porpoise was heard "talking" at frequencies ranging from 150 to at least 155,000 cps. The possibility of echo-ranging by the bottlenosed porpoise has been suggested by Kellogg and Kohler, who in a more recent paper (Kellogg, Kohler, and Morris, 1952) presented evidence indicating that two types of sounds produced by this species possess the characteristics necessary for a frequency-modulated type of echo-ranging and a pulse-modulated type, respectively. However, Schevill and Lawrence (1952) stated that they have sought for and failed to find evidence of echo-ranging.

Whatever the meaning, or meanings, of porpoise phonation, the great specialization of the acoustic apparatus of porpoises (Sinclair, 1950) would seem to indicate that aural stimuli are of considerable importance to these animals.

The present contribution, which is concerned only with porpoise sounds that are audible to the human ear, supplements the earlier findings of McBride and his co-workers with regard to *Tursiops,* and includes new material on the spotted dolphin or porpoise, *Stenella plagiodon*. The sounds under consideration have been included in a 10 inch disc recording published by the Marineland Research Laboratory (Wood, 1952).

The findings here reported were made with the aid of a U. S. Navy underwater sound projector type CFF-78187 which is capable of both pick-up and transmission of sound water. An amplifier, speaker or head phones, and tape recorder constituted the remainder of the equipment. The projector, used as a hydrophone, was suspended in the circular porpoise tank at Marine Studios during the earlier part of

this work, and later was installed on the floor of the tank. This tank is 75 feet in diameter, 12 feet deep, and supplied with portholes for underwater viewing. During the period covered by this report the cetacean population of the tank consisted of ten bottlenosed porpoises of both sexes, both adult and immature (the youngest approximately two years old), and two male spotted porpoises, one of which was apparently not yet full grown. Four of the bottlenosed porpoises had been born in the tank; the two spotted porpoises were relative newcomers, having been captured about six months before these observations were begun.

This tank also contains a number of fishes, including such known noise-makers as grunts (Family Haemulidae), sea bass (*Centropristes*), and trigger fish (*Balistes*). However, any sounds which might be produced by the fishes are not likely to be confused with the distinctive and much more varied sounds made by the porpoises.

The disadvantages of working with 12 porpoises of two different species at the same time are fully appreciated. Despite this situation it is often possible to identify the sounds of a particular individual, either by means of the air bubbles that usually accompany whistling and one other sound, by slight movements of the blowhole, or by the animal's proximity to the hydrophone. The difficulty of assigning specific sounds to a particular animal would exist in any arrangement involving more than one individual, since some of the sounds are produced with no outward indication that they are being made. Porpoises are gregarious by nature and an isolated animal is, in our experience, considerably less soniferous than a member of a group.

In the following section the principal sounds (within the sonic range) attributable to the Marineland porpoises will be listed. Except as noted, reference is to *Tursiops,* since this species is apparently more vociferous than *Stenella.*

The kind encouragement of Mr. William E. Schevill, Woods Hole Oceanographic Institution, is acknowledged with gratitude. I am also indebted to Dr. William S. Tavolga, City College of New York and American Museum of Natural History, for many helpful criticisms and suggestions.

Types of Sounds Produced and Attendant Circumstances

Jaw Clap.

This sound, made by clapping the jaws together, is a flat, abrupt noise similar to that which can be made by striking the palms of the

hands together. It is quite loud and can readily be heard through the walls of the tank. A jaw clap can often be attributed to a particular individual since the movement of the jaw is readily discernible.

This sound is frequently heard during the regular feeding periods, and most often emanates from the oldest (and probably the only fully mature) male *Tursiops,* an animal whose dominance over the others has not, up to the present, been seriously disputed. The jaw clap apparently represents threat or warning. There has been no indication that it is ever a part of the behavior of the spotted porpoises, but this may be because the two specimens of *Stenella* are outnumbered and apparently dominated by the bottle-nosed porpoises.

The sound of the jaw clap is not readily distinguishable from that of a tail blow, when one porpoise strikes another with its flukes.

The jaw clap was one of the three different sounds briefly noted by McBride and Hebb (1948). Our own observations support their interpretation of this sound as a form of intimidation by a dominant animal toward subordinates.

Whistling.

To the unaided ear whistling is the most frequently heard and the most readily audible of the sounds produced by *Tursiops.* Whistles are generally of short duration, seldom lasting a second, but not infrequently one whistle is followed by another with scarcely a pause between the two. Inflection may vary but is usually slight. Whistles are always high pitched, ranging up to at least the upper frequency limits of the human ear. They are generally clear and musical, although those of higher frequencies might better be termed squeaks rather than whistles.

Whistling is heard when the porpoises are playing and sometimes when they are simply swimming at a moderate rate around the tank. However, whistling also appears to be associated with certain emotional states. The greatest volume of whistling ever heard by the writer occurred when a seven foot sand-bar shark *(Eulamia milberti)* was introduced into the tank. For some minutes the porpoises, obviously excited, bunched together and stayed well away from the shark. Then some of them began to make sudden passes across the shark's bow, causing it to swerve sharply to one side. The loud and almost constant whistling continued for an hour or more. Unfortunately the hydrophone was not in commission at the time and no recordings were made. Two weeks later, with the underwater listening equipment

installed, a second sand-bar shark was placed in the tank. The volume of sound did not rise above that normally heard. The porpoises, having become accustomed to the presence of the first shark to the extent of using it now and then as a plaything to be pushed about, ignored the second shark almost completely.

Several months after both sand-bar sharks had died, a six foot tiger shark *(Galeocerdo cuvier)* was introduced into the tank. Again the porpoises exhibited signs of excitement, bunching together, staying in that part of the tank farthest from the shark, and speeding up their already accelerated swimming whenever they came closest to the shark. Considerable whistling was heard, but also rasping and barking sounds. The volume of vocalization increased markedly whenever the porpoises came closest to the shark. However, within 20 minutes they had apparently become accustomed to its presence and accorded it little more attention.

Introducing almost any strange or unfamiliar object into the tank will result in manifestations of excitement. But under such circumstances whistling is relatively infrequent and another type of sound, described below, is predominant.

Young *Tursiops* whistle more than older animals, and a young animal that is accompanying its mother whistles almost constantly when separated from her. On one occasion three wild bottlenosed porpoises were captured for experimental purposes and temporarily lodged in the flume connecting the two large exhibition tanks. One of these animals, a young male whose mother had escaped at the time of his capture, whistled repeatedly. The other two were an adult female and her still nursing daughter; as long as these two remained together whistles were seldom heard from either.

Whistling is one of only two sounds definitely attributable to *Stenella*. The younger of the two males whistles frequently, usually emitting two identical sounding whistles, each with a slightly falling inflection, and with a just perceptible pause between the two sounds. For some time it was believed that this type of whistling was produced only by the younger *Stenella,* but more recently it has been observed that the young bottlenosed porpoises are capable of emitting what seem to be identical sounds.

McBride (1940) first noted that whistling appears to be correlated with excitement and varies with "different emotional states." McBride and Hebb (1948) considered whistling one of the noises with "language" value (language in the sense that a dog's barking or

growling is language). They cite the occasion on which a mother and daughter *Tursiops* were temporarily separated by the shallow flume. The young animal whistled constantly and the mother is said to have answered frequently, remaining close to the gate of the flume until the water was lowered. When the continuity of the sound conducting medium was broken, the mother porpoise is reported to have left the gate and even to have taken an interest in catching fish.

McBride and Kritzler (1951) told of a mother *Tursiops* which, upon discovering the absence of her infant, would remain in the same location and begin to whistle. As soon as the young one returned her whistling would cease.

Rasping and Grating Sounds.

In this category are included a wide variety of sounds which apparently intergrade to a considerable extent. They may range from a brief, toneless, grating noise to a high pitched, rather musical meandering lasting two or three seconds. There has been no indication that the production of sounds in this category ever involves the escape of air from the blowhole; nor is there any other visible indication when such sounds are being made.

Only very rarely may sounds of this type be heard without the aid of underwater listening gear. It was not until the hydrophone was used that the abundance and the variety of such sounds became known.

When the hydrophone was first lowered into the tank the porpoises avoided it as they avoid any strange object. Within a few minutes, however, some of the younger bottlenosed porpoises began to swim close by it, craning their necks to peer at the instrument, and sometimes pausing before swimming on. During the approach or the pause a rasping or grating sound was heard that varied with different individuals and at different times, but frequently resembled the noise made by the rusty hinges of a slowly swinging gate. The duration of this sound generally ranged from one to three seconds; it was most prolonged when a porpoise paused to investigate the hydrophone.

It soon became apparent that the "rusty hinge" sound can be induced by introducing almost any strange (to the porpoises) object into the tank—for example, a white enameled pail, a dumbbell-shaped sound projector, a length of pipe, etc.

The general pattern of behavior under these circumstances is always the same; the porpoises bunch together and swim at a faster

Photo by Frank Essapian

FIGURE 1. Two bottlenosed porpoises investigating the hydrophone which, as a strange object, elicits the "rusty hinge" sound.

rate around the tank. They accelerate while passing the object, but crane their necks to look at it as they go by. Rasping sounds, usually brief, are heard at this time. Generally within only a few minutes (the Marineland porpoises have been subjected to many unfamiliar objects) their swimming slows and the younger animals (those which were born in the tank) approach the object more closely, and even pause and appear to examine it. If it is the hydrophone they are examining, the "rusty hinge" noise and related rasping or grating sounds are, of course, quite pronounced when heard through the listening equipment.

When the porpoises have become accustomed to the presence of an object they generally either ignore it or test its possibilities as a plaything—as something that might be pushed about the tank. In either case the object no longer induces the characteristic sounds heard earlier.

However, on one occasion, at night, loud and rather prolonged rasping and grating sounds were being emitted spontaneously by a number of the porpoises; at the same time the animals could be observed moving slowly near the bottom of the tank, nosing about the rock formations, and sometimes pushing or lifting rocks with their snouts. Their activity gave the impression of being investigative in nature. Porpoises are inquisitive and playful, and individual animals may often be observed poking about the rocks, but the sight of all or most of the porpoise colony (with the probable exception of the two spotted porpoises) participating simultaneously and apparently deliberately in such activity was distinctly unusual.

The two specimens of *Stenella* have not been known to produce sounds that may be included in this general category. It is entirely possible that they are capable of emitting such sounds, but it may be significant that the two spotted porpoises have not been observed to exhibit interest in the hydrophone or in other unfamiliar objects introduced into the tank. Their initial reaction may be that of fright or excitement, and, in company with the bottlenosed porpoises, they may give the object a wide berth for a while, but at no time have they exhibited curiosity or investigative behavior comparable to that shown by *Tursiops*.

A previous reference to odontocete phonation of this type is contained in Kritzler's paper on the pilot whale. Kritzler described a peculiar grating snore, produced only under water, and detected only with the aid of the hydrophone. It is of interest that he compared this sound with that made by a door swung on rusty hinges; almost the same comparison occurred to the writer the first time he heard the "strange object" sound of *Tursiops*, sometime before Kritzler's paper was published. Kritzler did not mention the circumstances under which this sound occurred.

Combined Mewing and Rasping Sounds.

Although related, at least so far as the human ear is concerned, to the preceding category, the type of phonation indicated by the above heading is so characteristic of one particular activity of the porpoises that separate grouping seems justified.

During regular feeding programs at Marine Studios a diver enters the circular tank and distributes fish to the porpoises from a metal basket. As soon as this feeding begins, a constant, subdued combination of rasping and mewing sounds is heard. When the last fish is gone

the diver raises the empty basket above his head. The porpoises, which have been clustering about the diver, immediately leave him and exhibit little further interest in his presence; at the same time the undercurrent of sound ceases or diminishes quite abruptly.

This complex of sounds is not heard when the diver is in the tank for any purpose other than feeding, but it may readily be induced by dropping a bucketful of fish into the tank when the diver is not present. Again the sounds cease when the fish have all been consumed. In both types of feeding the volume of sound seems to vary directly with the amount of fish being made available to the porpoises at any one time.

This distinctive rasping and mewing is audible only with the aid of underwater listening equipment. Unless some of the *Delphinapterus* sounds described and recorded by Schevill and Lawrence correspond to this particular phonation, it has previously been noted only in the disc recording "Porpoise Sounds" (Wood, 1952).

Barking

Occasional barks, along with occasional whistles, rasps, and other less easily described noises, are heard when the porpoises are playing, feeding, participating in sexual activity, and following such other pursuits as are available to them. There has been no indication what significance, if any, may be attributed to such random vocalizations.

Repeated barking (or what, onomatopoeically speaking, might better be described as a cross between barking and yapping) is a distinctive sound that is less frequently heard. From two to a dozen or more barks are repeated rapidly, generally with a slightly falling inflection, and such series of sounds may be repeated again and again with only a very brief pause separating one series from another. It is difficult to determine whether more than one animal is participating, but the effect is sometimes that of a chorus of barking sounds.

At one time barking was frequently heard when the basket of fish was placed on a platform just above the water for the diver to take down later. The porpoises always notice the arrival of their food and swim to the platform. However, barking is no longer heard when the fish appears, although the rest of the routine remains unchanged.

On only two occasions have particular individuals been identified as the source of barking sounds. Recently, at the same time that repeated series of barking sounds were heard (even without the aid of the listening equipment) the adult male *Tursiops* was observed

chasing the older *Stenella*. Streams of air bubbles were being emitted from the blowhole of the latter at intervals which corresponded to the sounds of the barking. The nature of the pursuit was not clear; it was our impression that the chase was good natured, but such behavior on the part of these particular animals has not been observed before. The barking and the concurrent activity continued for about two minutes. Later study of the tape recording made at the time indicates that at least one other animal, in addition to the older *Stenella,* was also emitting barking sounds at the same time.

The other occasion on which repeated barking could be attributed to a particular individual occurred when the tiger shark (referred to under Whistling above) was introduced into the porpoise tank. Approximately ten minutes after the shark had been placed in the tank the younger spotted porpoise began passing it from the rear and, after swimming ahead of the shark, turning back to repeat the maneuver. At the same time barking was heard, with streams of air bubbles emerging from the blowhole of the porpoise at intervals corresponding to the repeated series of barking sounds. The movements of the *Stenella* were clearly oriented with reference to the shark. However, the porpoise did not approach the shark closely, and the significance of its behavior and vocalization was not apparent.

McBride and Hebb (1948) mentioned barking as one of the sounds made by *Tursiops,* but did not describe the sound further, nor did they indicate under what circumstances barking was heard.

Yelping

During the spring months sexual and mating activities are more prominent than at any other time of year; the available evidence indicates that conception normally occurs during this period. (See McBride and Hebb, 1948; McBride and Kritzler, 1951). In February and March, repeated, loud, high-pitched yelping sounds, similar to those that might be made by a young dog, have been heard. These yelps have been identified as coming from the adult male *Tursiops,* the dominant animal in the porpoise colony, and probably the parent of all the young conceived in the tank. Slight movements of this animal's blowhole have been observed to occur simultaneously with the yelping sounds, and on occasion one or another of the females has apparently responded to these sounds by joining the bull.

Yelping has previously been reported as part of the sonic repertoire of *Tursiops* by Wood (1952).

Other Sounds

A variety of other sounds have on occasion been heard, many of them similar to the white whale phonations reported by Schevill and Lawrence (1949; 1950). These include chirps, grunts, squeals, snorts, clucking noises, sounds similar to those made by a bulb horn, brief sounds reminiscent of the human voice, and others for which descriptive terms are wholly inadequate or lacking. Some of these may be variants of the sounds described above, but others would probably fall in categories not listed. In any case, they have not been correlated with any particular circumstances or any special behavior. The best that can be said at present is that they are generally heard when the porpoises are active.

Discussion

High-pitched whistling is known to be produced by *Tursiops, Stenella, Delphinus, Globicephala, Delphinapterus,* and probably other delphinids. It may, as remarked by Kritzler (1952) be found to be characteristic of odontocetes generally. McBride and Hebb (1948) considered it a sound having "language" value, and McBride and Kritzler (1951) referred to "the high pitched whistling which all dolphins observed by us use for ordinary communication."

There appears to be good evidence that whistling may constitute a form of communication between a mother porpoise and her infant, enabling one to find the other in the event of separation, but the whistling that is characteristic of excitement and that accompanies play, sexual behavior, and other activities may possess no more meaning than some of the shouts and cries of small children at play. The whistles occasionally emitted by animals that are simply swimming in normal fashion around the tank may constitute another sub-category of this sound, and are of interest because they are produced in the absence of any perceptible stimulus. Porpoises are gregarious animals and it may be that whistling sounds are normally utilized to maintain contact between individuals under circumstances of poor visibility—a condition which holds in many of the waters inhabited by these animals. Kellogg, Kohler, and Morris (1953), who analysed certain sounds produced by the bottlenosed porpoise, found that whistles may range in frequency from about 7000 cps up to at least 20 kc, and that these whistles possess the physical characteristics required for a kind of frequency-modulated echo-ranging. However, whether

porpoises actually utilize whistles for echo-ranging has not been demonstrated.

Of considerable interest are the rasping and grating sounds of which the "rusty hinge" noise is a prominent example. As noted above, phonations in this rather broad category are definitely known to be produced by *Tursiops,* but have not, on the basis of observations to date, been attributed to *Stenella.* So far as the phonic capabilities of the later species are concerned this negative evidence is of dubious value, especially in view of the small number of specimens under observation. Nevertheless, there may be some significance in the fact that the "rusty hinge" sound is clearly associated with investigative behavior or manifestations of curiosity on the part of *Tursiops,* whereas the spotted porpoises neither exhibit particular interest in unfamiliar objects, nor, apparently, produce this type of sound.

If the "rusty hinge" sound has meaning or function this is not deducible on the basis of the available evidence. Kellogg, Kohler, and Morris (1953) conclude from their analysis of such sounds that rasping or grating noises (described as a rapid series of "clicks" or "clacks" with very high frequency components) possess the characteristics necessary for a pulse-modulated type of echo-ranging, and the behavior of *Tursiops* at the time it emits these sounds certainly suggests that they might be used for echo-location or even what might be termed "echo-investigation." However, it remains to be demonstrated that the porpoise actually utilizes any of its phonations for this purpose. All of the available evidence is circumstantial, and speculation, though tempting, should be tempered with caution.

Similarly, with regard to the other sounds described in this paper, no definite conclusions can as yet be drawn. The repeated barking by *Stenella* seems to be induced by certain external stimuli, but no pattern is apparent. The yelping sounds heard during the period of increased sexual activity are known to be produced by the dominant bull *Tursiops,* but their significance is not entirely clear.

A comprehensive program for further study would require observations under controlled conditions (at least to the extent of segregating species) and analysis of the various sounds with the aid of precision electronic equipment.

Although our knowledge of the phonic proclivities of the spotted porpoise is based on direct observation of only two specimens, both male, there are indications that this species differs considerably from *Tursiops* in respect to sound production. This apparent dissimilarity

may bear some relation to certain ecological differences between the two species.

Tursiops is an inshore or coastal form. It often frequents shallow bays, estuaries, and other brackish tidal waters, even penetrating far up rivers. In such waters visibility is generally poor, sometimes no more than a few inches.

Stenella is an offshore porpoise usually encountered some distance from land. Visibility in the waters it inhabits is generally much superior to that of the bottlenosed porpoise's usual environment.

This comparison suggests that phonation generally, for whatever purpose, may be of greater importance to *Tursiops* than to *Stenella*. It should be noted that the beluga, which also is found in bays, estuaries, and rivers (Vladykov, 1944), is quite comparable to *Tursiops* in volume and variety of phonation. An anatomical comparison of the aural and phonetic mechanisms of these three forms might prove of considerable interest.

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FACTORS CONTROLLING MARINE INVASION INTO FLORIDA FRESH WATERS

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Abstract

Survey of the pattern of chlorinity and inland distribution of marine organisms in Florida suggests that Pleistocene sea level changes have been responsible for extensive areas of oligohaline water (100-1000 ppm Cl) and nearly oligohaline water (25—100 ppm Cl) on the peninsula accompanied by extensive invasions of blue crabs and marine fish. Transplantation experiments in nature indicate that sodium chloride in the oligohaline concentration range is important to survival. These experiments and a series of natural experiments support the idea that oligohaline waters and distance from brackish water determine the distribution of blue crabs and other marine forms in fresh water. The range and extent of osmoregulation for the blue crab is shown by blood analyses to account for their ability to make inland invasions. Evidence exists supporting the idea that oligohaline waters of the world are zones of evolutionary adaptive exchange between fresh and salt water. Such waters occur on porous land below 25 ft. elevation, in volcanic areas, and in arid regions with outlets to the sea.

In the unique and varied waters of the Florida penninsula a combination of geological circumstances has produced an unusual distribution of salt and extensive invasions of fresh waters by marine fish and crabs. These two phenomena seem to be related. Because of the geochemical distribution of the chlorides in the sediments an extensive series of lakes and streams exists which are not brackish but can hardly be classed as typically fresh either. These waters with chlorinities between .1 and 1 part per thousand (100 to 1000 ppm or .5 to 5% of full sea water) are best termed oligohaline as named by Redeke in 1922 (Hedgpeth, 1951). These waters lack the sharp fluctuations of estuarine waters. A study of these patterns in relation to the physiology of marine animals suggests new ways of considering how marine organisms are distributed inland and how the evolution of adaptations to aquatic environments has occurred.

Geochemistry of Salt in Florida Fresh Waters

Normally, the sodium chloride content of fresh waters is small, the chlorinity ranging from one to 10 parts per million. This chloride content is primarily the chloride content of the rain and decreases markedly with distance from the sea (Clarke, 1924). Many authors have found varying chlorinities of this magnitude in rains of different

types and in different areas. Larger chloride contents are found in natural waters under the following circumstances:

First, if the water passes over strata containing salt deposits or if it receives ground water contribution derived from salt laden strata, a much higher salt concentration may occur.

Second, water receiving components from volcanic areas especially those containing hot springs may contain high salt content.

Third, the concentration of waters by evaporation in the closed basins of arid regions and to some extent in the lower reaches of rivers in semi-arid areas may produce high salt contents. The ocean is a case of accumulation of salt in a closed basin.

Fourth, some chloride may be added to natural waters by pollution from sewage or industrial wastes.

Examples of these circumstances and summary of knowledge on the geochemistry of chlorine are available in Rankama and Sahama (1950).

In Florida it is primarily the salt deposits held in the sediments which have produced a pattern of high chlorinity in the fresh waters. Geologically, Florida is a dome of Tertiary sediments, mostly limestone, which is flat and scarcely elevated above the sea. The relative absence of impermeable strata has permitted extensive artesian aquifers to develop that cut across the formations of different age. The whole peninsula behaves like a sponge in which water is poured on top and flows out the sides through springs and ground water flow into the surface streams. Recent studies by Ferguson, Lingham, Love, and Vernon (1947), Cooper and Stringfield (1950), Black, Brown, and Pearce (1953) have established much about the nature and behavior of Florida ground waters.

Figure 1 is a simplified elevation may of Florida with 20, 50 and 100 ft. contours drawn. The areas below 20 feet in elevation are shown with wave-like shading to emphasize their position. There is abundant evidence (Flint, 1947) that at times in the late Pleistocene during warmer times the ocean level has been higher than at present. A distinct strand line about 25 ft. above present sea level is known as the Suffolk scarp and is marked by sand dunes known as the Pamlico formation. The 20 ft. contour line in Figure 1 corresponds roughly to a map of the Pamlico shore line by Cooke (1945).

Under conditions thus estimated to exist in the late Pleistocene, marine seas would have existed in the wave-like shaded areas of

FIGURE 1. Topographic map of peninsular Florida showing 20 ft., 50 ft., and 100 ft. contours. The area with wave-like horizontal shading below 20 ft. in altitude was submerged in Pamlico times and now tends to have higher chlorinities and marine invasion.

Figure 1 and the porous sediments beneath would have become infiltrated with salt water.[1]

At present fresh water extends downward in central Florida several thousand feet since a foot of fresh water above sea level can support a displacement of the salt water—fresh water boundary downward 40 feet according to the Ghyben-Herzberg approximation. Under the

[1]A suggestion made at the Fla. Acad. of Sci. meeting in 1951, at Amer. Soc. of Limn. and Ocean. meeting in 1952 but independently by Black, Brown and Pearce (1953).

circumstances shown in Figure 1 there could neither be fresh water in the sediments below the salt water sea areas nor artesian outflows that could wash out salt deposits already existing in the buried sediments.

Cooper and Springfield (1950) published a map showing the present distribution of salt in the ground waters in Florida. The areas of ground water salt greater than 100 ppm correspond almost exactly to the low areas of the peninsula shown as submerged in Figure 1. This suggests that the high salt content of the ground waters has relatively recently been left in the sediments perhaps during Pamlico time. The area of salty ground water cannot have been long raised and still contain salty ground water, for cores do not show corresponding reservoir beds of salt or evaporite deposits of arid climate in the recent rocks which underlie these salty areas. Furthermore the distribution of this salty water does not correspond to geological formations. The lack of extensive salt inside of the 20 foot contour suggests that a considerable time lapse occurred between times of higher sea levels and the time of the Suffolk Scarp.

The salt is working out at a rapid rate and the following calculation suggests that the rate of flushing out of salt is consistent with a hypothesis of Pleistocene salt deposition.

From a drainage basin of about 3000 square miles of the St. Johns river, the average runoff is 14.0 inches. If the runoff is assumed to contain in addition to cyclic salt 100 ppm chloride, a reasonable minimum value as shown in Figure 2, then 3.5 grams chloride per square centimeter per 1000 years is found to be flushed out of the area. If the pore spaces in the mainly limestone sediments are assumed to be 1% as a lower extreme and if these spaces are assumed to have been permeated with salt with a chlorinity of 19 parts per thousand, then 610 ft. of sediments would be flushed out on the average every 1000 years. For a porosity of 10%, 61 feet would be flushed out. Possibly the correct value for relatively unconsolidated limestones lies in between (Imbt, 1950). If porosities are higher, correspondingly longer times are required to remove the salt.

The water being flushed out has its ions in ratios different from those of sea water. As pointed out by Matson and Sanford in 1913 (Black, Brown, and Pearce, 1953), there is a higher calcium concentration than magnesium concentration which can be accounted for by an hypothesis of dilution of the original salts and solution of additional calcium. Similarly the strontium: calcium ratio is lower than in sea

water. Six unpublished analyses by Odum and Parrish indicate that there is a lower B/Cl ratio than in sea water thus suggesting that there have been other types of modifications. Black, Brown, and Pearce (1935) in their detailed account of salt water intrusion have made a careful analysis of ionic ratios in Florida ground waters. They call the ground waters with lower salinities than sea water "residual" using the name "connate" for water supposedly originally trapped and of higher salinity than sea water. But it seems possible that the presence of higher salinities than sea water may be associated with definite crystalline salt deposits or depositions under conditions of higher salinity than now exist in or around Florida. These higher salinity waters are mostly in deep or non-artesion strata and do not affect the surface pattern of oligohaline waters. The concentration of ground water salt should be helpful in constructing a paleo-climatic scale for the excess of precipitation over evaporation.

250 new analyses of chloride by the Mohr method in Florida surface waters made during summer 1952 have been combined with 230 analyses summarized from the literature by Black and Brown (1950) as the data upon which Figure 2 is based. Black Laboratories, Gainesville, Fla. and E. Chamberlain, Fla. Game and Fresh Water Fish Commission have other Cl data not used here. Because of limitations of space the raw data and the maps by river systems with the plotted chloride figures are not included but are filed and catalogued in the Dept. of Biology library, Univ. of Florida, Gainesville, Florida. By river systems this Cl data is summarized briefly as follows:

The St. Johns River at its headwaters has 31 ppm increasing to between 150 and 200 ppm between Lake Washington and Lake Harney becoming 227 ppm in Lake Monroe, 98 ppm just south of Lake George, 100-200 ppm northward to Palatka being less than 300 ppm to Jacksonville at times with values to 900 ppm at other times at Green Cove Springs and northward. Tributaries from the west off higher ground have chlorides less than 12 ppm such as the Oklawaha (except values of 50 ppm in lower east west section), Black Creek, and the Econlochatchee. The most extensive marine invasions occur in the St. Johns system apparently due to the salty springs which add salt such as Salt Springs, Silver Glen Springs, Ponce De Leon Springs of Volusia Co., Blue Springs at Orange City, Alexander Springs, and many salty artesian wells. For locations see Ferguson, Lingham, Love, and Vernon (1947).

The south Florida canals leading out of Lake Okeechobee have

about 35 to 100 ppm Cl. The rainwater of the central Tamiami Canal is lower being 13 ppm. Cl running north from the town of Everglades in the Rt. 29 canal decreases to 945 ppm at Rt. 41 junction, 116 ppm 4 miles north of this and 38 ppm 10 miles north of the junction. Lake Okeechobee varies 16 to 60 ppm as do the main

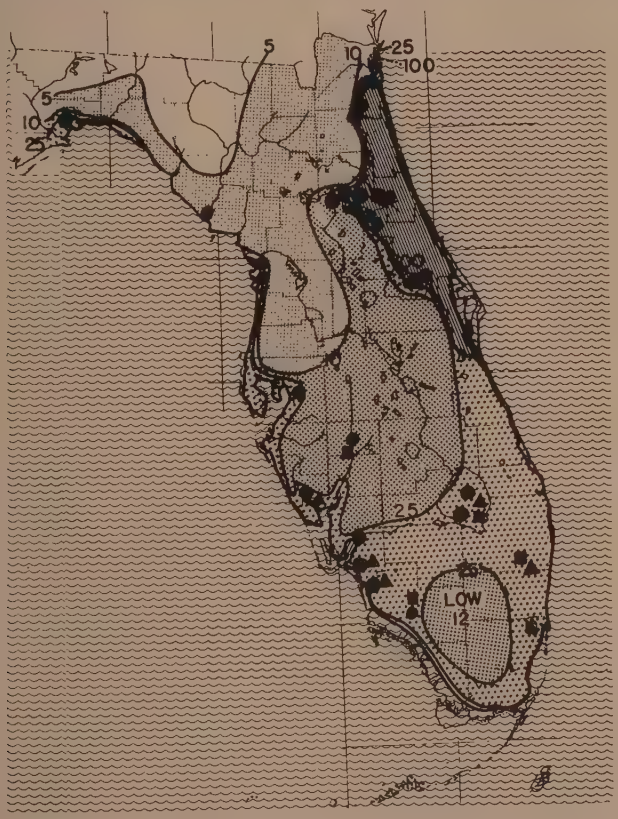

FIGURE 2. Surface chlorinities in lakes, streams, and canals given in parts per million. Somewhat smoothed isochlor lines (5, 10, 25, 100, and 1000 ppm) are drawn on the basis of 480 analyses scattered over Florida: Small stippling, 5—10 ppm; medium stippling, 10-25 ppm; large stippling, 25—100 ppm; vertical hatching, 100—1000 ppm; horizontal wavy shading, greater than 1000 ppm. Places of marine invasion are indicated for 4 indicator species: Blue crabs, solid circles; snook, squares; tarpon, triangles; sting ray, dot in circle.

outflows through the St. Lucie canal and the Caloosahatchee River. Estero and Imperial Rivers south of Ft. Meyers have more than 1000 ppm apparently of ground water origin. The drainage into Lake Okeechobee from the north through the Kissimmee, Indian Prairie Canal and Fish Eating Creeks has less than 23 ppm.

The Peace River system is low in Cl generally 16 ppm or less. The small rivers with mouths on Tampa bay are less than 12 ppm in headwaters increasing to 30 ppm 5 to 10 miles from the mouth. The Withlacoochee river draining central Florida is low, 13 ppm or less. The group of spring runs opening separately on the West coast is described below.

The Suwanee-Sante Fe system is low in chloride being generally 8 ppm or less. Similar low values characterize the pan handle rivers except where the small streams pass over low ground in the last 5 miles.

Estuaries throughout the State are typically 1000 ppm or over including 11,000 ppm in the Indian River and 15,700 ppm among the mangrove islands and lakes of the lower everglades region.

The map in Figure 2 is a smoothed summary. Clearly the chloride content of surface waters reflects the chloride content of the ground waters as observed in a comparison of Figures 1 and 2. The contrasts between low and high salty regions are especially prominent between streams entering the west and east sides of the lower (northern) St. Johns river. Single analyses of streams can be compared with some validity where there are sharp contrasts in chloride content, although it must be kept in mind that the chloride content of a stream may vary markedly with the season. The low chloride surface waters of north central Florida and the central everglades are mostly rainwater. Woodcock (1952) collected rain from south Florida with chlorinities from 1 to 10 ppm inversely depending on the intensity of the rain.

Although the evaporation rate in Florida is high, the accompanying high rainfall prevents the evaporation from producing any large concentrating effects. The role of evaporation increasing the salt content depends on the percent turnover of the body of water. Mr. A. O. Patterson, District Engineer, Surface Water Branch of the U. S. Geological Survey at Ocala, Fla. has furnished evaporation data from their records on the large Lake Okeechobee. Between 1940 and 1946 there was an evaporation of 52 inches per year. A lake with no inflow other than rain and in a region with about 48 inches rain (Moorehaven 1940-1946, Records of Florida State Board of Conservation) would have the chloride of the rain concentrated many

times. Most of the Florida fresh waters have inflows, and the greater the inflow due to streams the less would be this concentration. The chloride figures give in Figure 2 suggest that concentrations of 1 to 10 times may occur. In Lake Okeechobee there is apparently a concentration in passage through the lake of not over 1-2 times on the average because the inflow and rain together much exceed the evaporation. However, rainfall variations from year to year range from 30″ to 75″ so that the action of evaporation is subject to extreme annual variations.

Because of the low elevation, tidal waves move as much as 60 miles up some of Florida's canals and streams. However the actual transport of salt of immediate marine origin does not proceed such a distance for the tide causes only a pulse but not a reversal of current direction. Good examples can be observed in Weekiwachee or Chassahowitzka Springs rivers. The oligohaline water far up the rivers and canals derives its salt from the ground water. How far marine salt comes upstream as wedges of bottom water in the St. Johns river is not yet known.

Invasion of Marine Fauna into Florida Fresh Waters

That many marine fishes and blue crabs come regularly up streams and springs in Florida for a much as 180 miles is common knowledge in the hundreds of fish camps throughout Florida. In the scientific literature numerous references to this invasion have been made, such as by Carr (1937) and Gunter (1942). Sixteen species of marine fishes were recorded from oligohaline Homosassa Springs by Herald and Strickland (1949). Members of the biology department of the University of Florida have gradually been establishing a detailed pattern of the distribution of marine invasion although the difficulty of the task makes it a long term project. Crab occurrence records are given for Florida by Rathbun (1930).

Without waiting for careful icthyological survey of all the State's waters it is possible to establish roughly the distributional pattern of some indicator species in order to compare with the distribution of oligohaline water. Data on marine invasion is derived from personal observations in springs, interviews throughout Florida during June 1952, Herald and Strickland (1949), Dequine (1953), and records of fishes and crabs held by the U. S. National Museum especially due to collections of E. S. Herald, now curator, Steinhart Aquarium, San Francisco, California.

Symbols representing 4 species (*Callinectes sapidus, Tarpon atlanticus, Centropomis sp.,* and *Dasyatis sp.*) in Figure 2 indicate the similarity in the distribution of marine invaders and oligohaline or nearly oligohaline waters. It is difficult to distinguish between sporadic and frequent occurrence but only occurrences reported several times are included. Quantitative data on fish catches in oligohaline Lake George and nearly oligohaline Lake Okeechobee (Dequine. 1953) indicate that the number of marine fish present is considerable. For example, 1,602 lbs. of croakers (*Micropogon*) and 7,911 lbs. of sting rays (*Dasyatis*) were harvested from Lake George in 1952 and 1,556 lbs. of tarpon (*Tarpon*) from Lake Okeechobee.

Over most of Florida, apparently no chloride limit exists for the following species: mullet (*Mugil cephalus*), 3 ppm in Ponce De Leon Springs, Holmes Co.; needlefish (*Strongylura marina*) 5 ppm in Weekiwachee Springs; and sole (*Trinectes maculatus*), 5 ppm in Ichatucknee Springs.

Other species seem to be limited in their inland distribution to oligohaline or nearly oligohaline water. Listed below for each species is the lowest chlorinity observed where frequent occurrence was reported. Snook (*Centropomis sp.*), 25 ppm in Hillsborough River, L. Okeechobee and the N. New River Canal, 12 ppm in the high sulfate Peace River; blue crab (*Callinectes sapidus*), 25 ppm in Alafia River and Oklawaha River, 12 ppm in the Peace River; tarpon (*Tarpon atlanticus*), 35 ppm in the North New River Canal and Lake Okeechobee; sheepshead (*Archosargus probatocephalus*), 30 ppm in middle Weekiwachee River; mangrove snapper, (*Lutjanus griseus*), 50 ppm in Chassahowitzka Springs; channel bass (*Sciaenops ocellata*), 100 ppm in Crescent Lake; croaker (*Micropogon undulatus*), 150 ppm in the St. Johns River; sting ray (*Dasyatis sp*), 150 ppm in upper St. Johns River; peneid shrimp (?), 150 ppm in central St. Johns River; snapper (*Lutjanus sp.*), 570 ppm in Homosassa Springs; sea trout (*Cynoscion nebulosus*), 570 ppm in Homosassa Springs; hydroid (sp.) reported by C. F. Byers from Homosassa Springs; barnacles (sp.?), 900 ppm at Green Cove Springs on the St. Johns River (larvae possibly released from ship bottoms); marine amphipods, 900 ppm in Chassahowitzka River.

Additional fish species occurring more sporadically are recorded in Herald and Strickland (1949), Dequine (1953), and will be in Carr and Goin's forthcoming *Guide to the Reptiles, Amphibians, and Freshwater Fishes of Florida.*

For the blue crab where the most observational data are available the following minimum chlorinities were recorded for invasion into various bodies of fresh and oligohaline water: Trout creek, 220 ppm; St. Johns River, 150 ppm; Crescent Lake, 96 ppm; Chassahowitzka Springs, 53 ppm; Lake Okeechobee, 35 ppm; Tamiami Canal, 35 ppm; Wakulla River (lower) 30 ppm; Crystal River, 25 ppm; Alafia River 25 ppm; Miami Canal, 24 ppm; Oklawaha River, 15 ppm; Peace River (high sulfate), 12 ppm; Weekiwachee Run, 12 ppm; Wekiva Spring River, Orange Co., 10 ppm; Green Cove Springs (100 yds from high salt) 5 ppm.

It seems clear from the field data that blue crabs will move very short distances into water with little chloride but occur frequently and abundantly only with 25—100 ppm Cl or more. Current and elevation may effect this migration but are apparently not the main factors in Florida as discussed below in numbered paragraph 3.

Natural Experiments which Relate the Distribution of Marine Invaders and Especially the Blue Crab to the Distribution of Oligohaline Waters

A number of distributional patterns are described below which help one to understand Florida marine invasion.

1. Blue crabs (*Callinectes sapidus*), especially males but not exclusively males move up into fresh waters from both the Atlantic and Gulf coasts. As observed during 1951-52 in Homosassa Springs and reported in other parts of the State, the maximum invasion is in the summer. Hay (1904) and Pearson (1948) find this to be the case in the Chesapeake Bay estuaries also. It is interesting that this seasonal pattern exists in Homosassa Springs in spite of the constant temperature of the spring. Florida crabs in commercial quantities range over 100 miles up the St. Johns River with its high content of salt which originates from ground water. At intervals of 25 miles or so there are large high chlorinity springs where the crabs may tank up much as an automobile enroute. The high density of marine forms in Homosassa Springs (570-800 ppm Cl) may be due to the pausing of the fish and crabs in the boils to tank up on salt, since they may be losing salt in the large broad feeding areas of the run immediately adjacent where chlorinities are somewhat lower (300 ppm Cl).

2. The tendency for crabs and fish to move most readily into oligohaline waters but to penetrate only short distances in the lowest chlor-

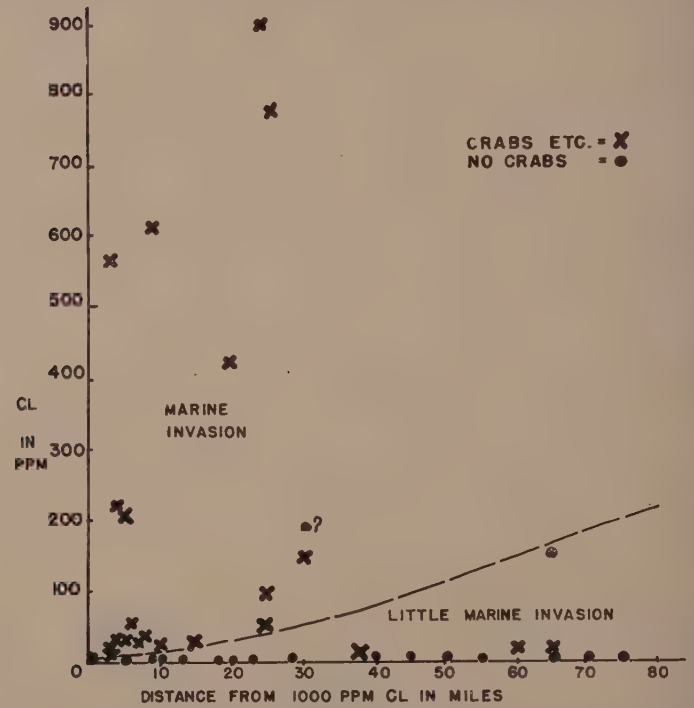

FIGURE 3. Bodies of fresh water which receive marine invasion and those which do not are plotted on a graph of chlorinity and distance from places of high chlorinity. Little marine invasion is associated with that part of the graph with lowest chlorinities and greatest distance from brackish water below the slanting line.

inity waters is demonstrated in Figure 3. Localities known to receive marine invasions or known rarely to receive them are plotted on coordinates of chlorinity and distance from chlorinities of 1000 ppm. It is possible roughly to divide these two types of localities by a slanting line that indicates that as distances from high salt become greater marine invasion requires higher oligohaline chlorinities. Four exceptions include a few crab records for Wekiva River, Oklawaha River, and Peace River discussed below and uncertain status of Alexander Springs.

3. In contrast to the St. Johns River the Suwannee-Santa Fe Rivers, which contain mainly the salt of rain water, do not contain many if any

crabs above the delta area. Low elevation and slight current are concurrent factors here probably favoring marine invasion in the St. Johns River or any other sluggish stream but are not definitive since some crabs go far up the fairly swift Peace River. They seem to be generally absent in the central Tamiami canal which is very flat. Currents are generally weak in the streams of peninsular Florida.

4. The crabs found up the Peace River as far as 50 miles from any salt other than rain water salt may be an exception due possibly to the strange chemical composition of this often polluted river with its high sulfate (64 ppm) and high phosphates (5 ppm). Over the earth high sulfate waters without high chlorides are rare so that even if sulfate can substitute for chloride it will rarely occur. Mr. Ellis Landquist from his interviews and collections along the Peace River in his study of pollution states that there is evidence that the crab invasion is a recent change. Crabs move into water with very low chlorinities in the Oklawaha and Wekiva River (Orange Co.). In the other waters of the State 25 ppm chloride seems to be a boundary for frequent occurrence and 100 ppm chloride for really abundant presence depending on the distance from even higher chlorinites. Most of these waters are hard with 40 ppm calcium or more so that chloride is the main variable, although magnesium and sulfate tend to be higher when the chloride is very high. Where waters are both soft and low in chloride as in many lakes and headwater streams there is no crab invasion as in the Tamiami canal. Even widely ranging species such as mullet are scarce in such waters. Thus the calcium and the corresponding alkalinity are probably factors here as reported in the literature (Krogh, 1939) although in most springs and stream waters the calcium is relatively constant (10-60 ppm) compared to the range of sodium chloride (5-2000 ppm).

5. That crabs are regulated in their distribution by the stimulus of the sodium chloride content as well as the tolerance is suggested by the crab distribution in Chassahowitzka Springs boil area. Although crabs were able to live 10-20 days in cages in the main boil with a chloride content of 50 ppm as described below, and although this boil area contains a dock from which fish heads are tossed as boats unload, crabs are only rarely observed to enter this area. In contrast crabs are abundant a few hundred feet down stream where a second spring with chlorinity of 730 ppm mixes with the first boil water. Thus this natural situation suggests that the sodium chloride is both a stimulus to selection of water in a gradient and physiological re-

quirement. It seems that in these low ranges, the sodium chloride is important qualitatively as well as in a role of increasing total osmotic pressure. The difference between 10 and 50 ppm chloride in water with 250 ppm total salts is not great as total solute but is clearly important to the distribution of marine invasion.

6. Perhaps the clearest demonstration of the salt role in marine invasion by the natural experiment method is a comparison of 4 spring runs: Weekiwachee, Chassahowitzka, Homosassa and Wakulla on the west coast of Florida. Each run is about 8 miles long gradually becoming an estuary in the lower parts. The calcium contents are almost identical at about 50 ppm. By coincidence the constant chlorides of the first three are respectively 5, 53 and 570 ppm. The distribution of marine invasion is similarly striking. Weekiwachee regularly has only the mullet, sole, and needlefish; Chassahowitzka has mangrove snappers and crabs up to the boil; Homosassa always has 500 or more individuals of 5—15 marine species milling around the boil. The Wakulla River begins as a low chlorinity spring without the oligohaline species but as it passes downstream and passes the 25 foot altitude and the Pamlico scarp, additional springs raise the chlorinity to 30 ppm. At this point blue crabs, fiddlers, *Potomogeton pectinatus* and other oligohaline forms appear.

7. It is possible that spring waters by their clearness and lack of organic matter attract marine invasion. If there is a tendency to respond to water of low turbidity and organic content, marine organisms might respond to spring waters and marine waters which tend to be similar in this respect.

8. In a personal communication, Harold Humm of the Oceanographic Institute, Florida State University, describes an extensively used procedure for killing blue crabs in a limp position by placing them in fresh water. He describes the complete failure of this procedure at Beaufort, N. C., Duke University Marine Station using local fresh well water. The crabs did not die. This may have been another example of the effect of small sodium chloride content.

9. In these discussions, a clear distinction should be made between marine species which invade fresh waters and those species of marine affinity completely adapted to permanent life in fresh water. Thus there are species of fresh water crabs in rivers throughout the world in waters with only the chloride content of rain water, such as the Blue Nile (Flower, 1931). A. M. Laessle of the University of Florida

has found a crab species in Jamaica Bromeliads. In Florida there is a small fresh water crab *Rithropanopeus harrisi* Gould (Rathbun, 1930) which is recorded a number of time from oligohaline waters in the St. Johns River. The osmoregulation is discussed below. The saber crab *Platychirograpsis typicus* which was described by Marchand (1946) as possibly introduced into the Hillsborough River near Tampa, Florida may be another oligohaline crab. It is at present distributed in the lower Hillsborough River and Sulfur Springs where the chlorinities are high for fresh waters. A specimen of *Sesarma sp.* was collected in Silver Springs in September, 1953. It is obvious that not all marine invaders are chlorinity sensitive since a few species of fish are found long distances up low chlorinity rivers like the Mississippi and the Amazon. (Gunter 1942).

Crab Survival Experiments

To test the abilities of Blue crabs to move into oligohaline waters some transplantation experiments were made both in Florida and at Woods Hole, Mass. Crabs were transported by car and were out of the water less than 2 hours in all experiments. In the Florida experiments sudden transfers from brackish water were made into hardware cloth cages in constant temperature springs. In the Woods Hole experiments crabs in 30 parts per thousand salinity were conditioned in 1/10 sea water for 24 hours before transferring to cages in ponds. Experiments on osmoregulation in crabs following sudden transfers summarized in Prosser (1950) suggest that 1-2 days are usually required for internal salt concentrations to reach a new equilibrium.

The results in Table 1 indicate that crabs can live longer in those freshwaters with higher chlorinities especially in the oligohaline range (.1 to 1.0 parts per thousand). In the Florida transfers the ability to survive is correlated with the natural presence of blue crabs in the springs used for the experiments. The crabs in the Woods Hole area have a similar ability to live some time in oligohaline water although such waters are scarce in the northeast. The ability of the Woods Hole crabs to survive in oligohaline waters of low alkalinity suggests that calcium is not a major factor.

Physiological Basis of Crab Invasions

Extensive series of experiments by many workers on many species of marine animals which can move with varying degrees into brackish water have permitted a general scheme to be established as to the

TABLE 1

TRANSPLANTATION EXPERIMENTS WITH BLUE CRABS

Crab Source, Date	*Cl ppm*	*Number of Crabs*	*Place of Experiment*	*Ca ppm*	*Temp. Deg. F.*	*Cl ppm*	*Days Survival*
IN FLORIDA SPRINGS, 1952:							
Bayport estuary, Feb. 4	3300.	7	Homosassa	50	75	570.	>14
Bayport estuary, Feb. 4	3300.	5	Chassahowitzka	49	74	53.	7-18
Salt Springs, Aug. 7	2800.	8	Silver	70	73	8.	5
Bayport estuary, Feb. 4	3300.	4	Weekiwachee	49	74	5.	1½
Bayport estuary, Feb. 5	3300.	4	Weekiwachee	49	74	5.	1
Chassahowitzka run, Aug. 22	730.	7	Rainbow	21	74	4.	1-2
PONDS AT WOODS HOLE, MASS., 1953:							
24 hours in lab., Aug. 13	1680.	3	Nobsca pond	9*	70-80	475.	9->18
24 hours in lab., Aug. 13	1680.	3	Rain pool at golf course	5*	70-80	11.	1

*Calcium values at Woods Hole inferred as .4 of Methyl Orange alkalinity

variation of internal salt with external salt. According to the shape of these curves Krogh (1939) and Prosser (1950) have summarized this data into types.

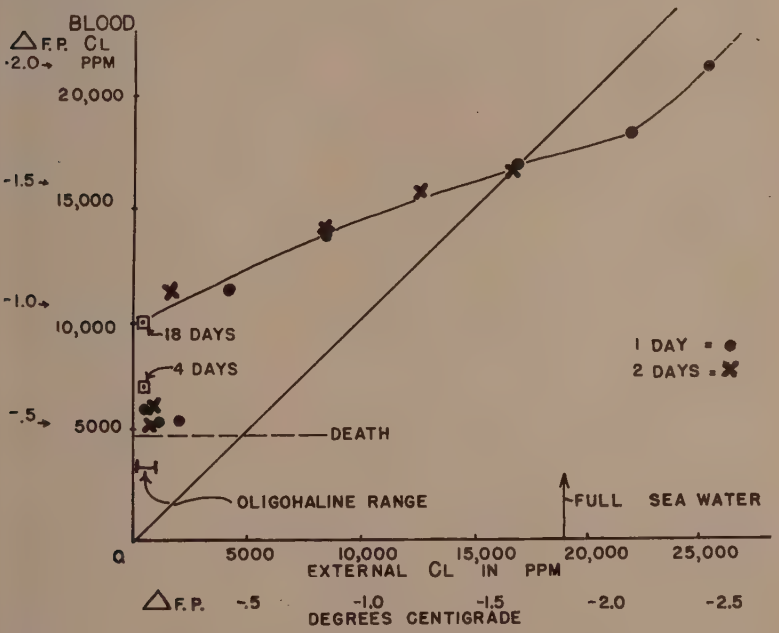

FIGURE 4. Internal blood chlorinity as a function of external chlorinity in the blue crab (*Callinectes sapidus*) at Woods Hole, Mass., August 1953. A roughly equivalent scale for lowering of the freezing point is given in degrees centigrade. The time lapse between start of each experiment and the measurement of blood chlorinity is indicated in days.

To check the characteristics of the osmoregulation of the blue crab, a few measurements were made of blood chlorinity as a function of external chlorinity after 24 and 48 hours dilution. These experiments were made with crabs collected near Woods Hole, Mass., and kept in frequently renewed containers. Figure 4 shows the general class of this curve is somewhat similar to the one for the Chinese wool-handling crab *Eriocheir sinensis* that has a similar ecological distribution in the low country of Europe. Scholles (Prosser, 1950) and Krogh (1939) indicated that *Eriocheir* regulates like a freshwater organism while it is up in the rivers. The blue crab belongs with the

group that is more or less isotonic at full sea water salinities but regulates at lower or higher salinities. The blue crab is isotonic at somewhat less than full sea water. If crabs are placed suddenly from 19,000 ppm into the very low chlorinities of the oligohaline range (450 ppm), they lose salt rapidly until death occurs at 5000 ppm blood chlorinity. If however crabs are acclimated one day in brackish water (2000 ppm) before introducing into the oligohaline water the regulation after an adjustment period is continued even at this low external chlorinity. A crab kept 2 weeks in 450 ppm chlorinity had an internal blood chlorinity in line with the slanting curve in Figure 4. Figure 4 includes blood analyses from individuals in the process of losing salt rapidly as well as those which were regulating. It seems likely that crabs can recover from some loss of chloride below their regulation levels following fairly sudden changes since they maintain considerable activity as long as chloride levels do not fall below 5000 ppm. A crab was active in one case with low internal chlorinity (6930 ppm) 4½ days after sudden shift to oligohaline water. Huf (1933) found 7000 ppm Cl in *Potamobius* blood from fresh water.

A curve of internal osmotic pressure against external osmotic pressure obtained by Jones (1941) for *Rithropanopeus harrisi* from low salinity waters in San Francisco indicates that the crabs can survive for some time with internal blood salts below the level of regulation. *Rithropanopeus harrisi* does not regulate as much as the blue crab.

Evolutionary Implications of the Oligohaline Range

The remarkable distribution of blue crabs and possibly other marine organisms in Florida fresh waters seems to be an ecological manifestation of the physiological phenomena described above and the extensive oligohaline waters. From the data at hand it seems likely that as an intermediate between typically freshwater and marine forms, the blue crab belongs to a class of organisms which can exist in fresh water only if they can obtain sufficient salt to compensate for that lost. Apparently the chlorinity range from 10 to 500 ppm is important for these organisms. As intermediates physiologically and ecologically these oligohaline organisms may represent intermediates in the evolutionary shift of species from freshwater to saltwater.

The penninsula of Florida is a block of sediments of a type which must have always existed in varying quantities somewhere through

geological time. It is a block of sediments which is exposed to oscillations of the sea and a consolidation process. The suggestion is made that in such environment gradual ranges of chlorinity have always existed without the sharp tidal salinity shifts of the usual estuary. Under such conditions it seems reasonable that evolutionary shifts of species from fresh water to salt water and back may have occurred readily. Certainly at present in the St. John's river and in the salt springs there exist fish communities with mixed components. Perhaps the line between fresh and salt has not always been so sharp. The Paleozoic formations containing fossil fishes now long since consolidated may have formed in environments with geochemical properties similar to those of modern Florida.

Marine fauna with a tendency to develop freshwater forms such the Mysid shrimps might be expected to make the transition readily where stable salinity gradients have persisted. It is interesting therefore that Horton Hobbs and Irene Bolick (unpublished) have found Mysids in Wakulla Springs and McLane (1948) found them in the St. Johns River since these two streams have stable oligohaline chlorinity grandients. Carr (1937) described 3 marine relict fish established in freshwater Lake Eustis.[2]

Geographical Implications of the Oligohaline Range

If, as this odd assortment of data suggests, the sodium chloride content of fresh waters is important in controlling the distribution of marine invasion in Florida in the oligohaline range, there are other areas of the world which might be expected to receive similar marine invasion and characteristic faunal associations.

Sedimentary and porous areas peripheral to the Suffolk scarp line of about 25 ft. present elevation may be expected to contribute springs and ground waters of relatively high chlorinity for fresh water and thus to encourage marine invasions.

The Netherlands, Belgium, and North Germany resemble Florida in some respects. Many of the fresh waters from these regions have chlorinities 10—500 ppm (Redeke, 1948). In fact the fresh-salt boundary based on faunal differences as defined by Redeke and Valikangas may have been much affected by the presence of much oligohaline water in their areas. Thienemann (1950) describes some

[2]Two recent papers read at the December 1953 Florida Academy of Science meetings at Rollins College have described additional marine invasion: (1) Wass, M. Two Mysid shrimps, one fresh water and one marine, previously unreported from Florida. (2) McLane, W. N. Notes on the fishes of the St. Johns drainage system.

marine invasion in this part of Europe. The artificially introduced Chinese wollhandling crab is centered in these areas. Other cases of other species are mentioned by this author.

The upper reaches of Lake Pontchartrain in Louisiana may owe its marine invasion (Gunter, 1942) to oligohaline water. In Belmonte, Cuba, Brues (1927) kept *Callinectes ornatus* in "freshwater" three months up Rio Caonao in a pond previously flooded with sea water. The caves of Yucatan whose aquatic fauna is partially marine contain fresh waters with the chlorinity range nearly oligohaline. Pearse (1938; Pearse *et al.*, 1936) who monographed this fauna nevertheless does not think of these low chlorinity waters as important to evolutionary exchange of fauna between freshwater and marine areas as the beaches (Pearse, 1952).

Rivers draining arid regions where evaporation and accumulated salt deposits contribute to the chlorinity should receive considerable marine invasion. Such waters as those in southwest Texas and southernmost California have chlorinities of the range which by this theory should encourage marine invasion. Salton Sea has marine forms and Gunter (1942) describes marine invasion for the Rio Grande. Most of the rivers of the United States that reach the sea however, have chlorinities less than 15 ppm chloride and are not oligohaline. Mansuetti (1952) reports that the penetration of some marine fishes in such low chloride rivers as surround the Chesapeake Bay is not much over 10 miles from tide water and high salinities.

Areas which receive chlorides in part from volcanic waters and hot springs and also are known to receive marine fishes (Herre, 1924) are found in the Phillipines such as Lake Manait, Lake Buhi, Lake Bombom, and Taal Lake with chlorinities of 580 ppm or over (Heise, 1917). Some marine relicts are described in low altitude lakes and the acidotrophic lakes of Japan and the Kuriles (Miyadi, 1933, 1938).

The often repeated idea that tropical waters receive more marine invasion than temperate ones seems open to the alternative suggestion that tropical waters more often contain appreciable oligohaline chlorinity.

Freshwater Invasion of Marine Waters

Most of the data in this paper concerns the invasion of freshwater by marine species but the oligohaline waters should favor the reverse migration also. Ordinarily when brackish water animals adjust to

freshwater they move from a sharply fluctuating salinity into a more constant environment. For a freshwater species to invade the usual estuary it must adjust to a condition of greater salinity oscillations and to a very sudden increase at the fresh-brackish boundary. Thus the usual estuary tends to be a barrier to freshwater species.

Gradual oligohaline gradients such as occur at the mouths of some of the oligohaline springs and the St. Johns River are much less a barrier and should favor invasions and evolutionary adaptation of freshwater species to marine conditions. William Sloan of the University of Florida has found evidence for this in his study of the insects in the spring runs of the west coast of Florida now in progress. Similar phenomena may be involved where the snail *Physa* occurs in the Baltic sea. Davis (1948) found considerable fresh water component in Long Lake in the brackish everglades at 15,000 ppm Cl.

Consider a range of chlorinity from 1.9 ppm Cl such as occurs in some rivers in eastern United States to 19,000 ppm Cl characteristic of the open sea. What may be important to an organism is the percent change. A change from 1 to 10 is as harsh as a change from 10 to 100 or 100 to 1000. Consider therefore the chlorinity range on a logarithmic scale. The range can thus be divided into 4 cycles each representing a 10 fold chlorinity change as follows:

No. 1	1.9	to	19.	ppm
No. 2	19.	to	190.	ppm
No. 3	190.	to	1,900.	ppm
No. 4	1,900.	to	19,000.	ppm

An oligohaline salinity gradient such as discussed above has the complete range represented by considerable areas without sharp daily change. Fresh water organisms dominate the first two cycles. Fresh water organisms and marine organisms share the third cycle. Only the fourth cycle is dominated by marine species. In the usual estuary, cycles 1, 2, and 3 are mostly absent being represented mainly by a sharply fluctuating boundary zone. Thus where the whole intermediate salinity range is present, it is not correct to say that marine components dominate the intermediate zones. Certainly the fauna of the salty springs is more fresh in affinity than marine even though the salinities are in the brackish range.

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